Gastropods from Upper Pliensbachian to Toarcian (Lower Jurassic) sediments of Causses basin, southern France, and their recovery after the Early Toarcian anoxic event

Category: Original Article

Roberto Gatto (corresponding author)

Dipartimento di Geoscienze, Università di Padova, Via G. Gradenigo 6, 35131, Padova, Italy.

Stefano Monari

Dipartimento di Geoscienze, Università di Padova, Via G. Gradenigo 6, 35131, Padova, Italy.

Pascal Neige

Laboratoire Biogeosciences, UMR CNRS 6282, Université de Bourgogne, 6 boulevard Gabriel, 21000, Dijon, France.

Jean-Daniel Pinard

Laboratoire Biogeosciences, UMR CNRS 6282, Université de Bourgogne, 6 boulevard Gabriel, 21000, Dijon, France and Musée National d'Histoire Naturelle, Section Paléontologie, 25 rue Münster, 2160 Luxembourg, Grand-Duchy of Luxembourg.

Robert Weis

Musée National d'Histoire Naturelle, Section Paléontologie, 25 rue Münster, 2160 Luxembourg, Grand-Duchy of Luxembourg.

Short title: Jurassic gastropods from southern France and T-OAE

Corresponding author e-mail: roberto.gatto@unipd.it

Abstract – A gastropod fauna has been studied from the Upper Pliensbachian to Upper Toarcian deposits of two sections of the Causses basin (southern France) in order to investigate the mode of recovery after the Early Toarcian anoxic event. The fauna consists of 15 species, one of which new, *Bathrotomaria kronzwilmesorum* sp. nov. Their stratigraphical distribution shows two peaks of diversity, i.e. in the Bifrons Zone, Bifrons Subzone, and in the Aalensis Zone, Mactra Subzone, which reflect brief times during which the oxygen content and bottom consistency favoured the settlement of a relatively diversified fauna. In the Variabilis to Pseudoradiosa Zones, gastropods are represented only by two species. This probably indicates more severe and unstable environmental conditions allowing survival only to gastropod taxa with wide adaptive capacities. The very low species diversity and the discontinuous and slow faunal recovery were probably determined by physiographic factors. The Causses area was a small basin confined by exposed lands and open towards the central part of western Tethys. Gastropods described here occur exclusively in the Toarcian–Early Aalenian communities of the European epicontinental seas, whereas species from the central region of western Tethys are absent. Geographic isolation and marginal location of the Causses basin restricted faunal exchange with the western European epicontinental seas, preventing fast recovery after the anoxic event. Gastropods of the central region of the western Tethys were probably unable to settle and colonize that area due to the strongly different environment.

Keywords**:** Gastropoda, Systematics, Lower Jurassic, Early Toarcian anoxic event, Palaeobiogeography, France.

1. Introduction

The Pliensbachian–Toarcian time span is marked in the Tethyan realm by palaeogeographic and palaeoenvironmental changes that had a profound impact on the marine biodiversity. The central region of the western Tethys was subject to a highly dynamic tectonic evolution driven by the

Neotethyan rifting which caused the establishment of areas with pelagic/carbonate platform sedimentation (e.g. Channell *et al*. 1979; Ziegler, 1988; Nairn *et al*. 1996; Ziegler & Horváth, 1996; Dercourt *et al*. 2000; Golonka, 2004, 2007; Santantonio & Carminati, 2011) and separate benthic faunas (e.g. Gatto & Monari, 2010; Gatto *et al*. in press and references therein). On the other hand, the stable European epicontinental shelf witnessed a period of environmental perturbations culminating with the widespread deposition of organic-rich sediments ('black shales') in the Early Toarcian (Röhl *et al*. 2001; McArthur *et al*. 2008; Hermoso *et al*. 2013 and reference therein). These sediments, such as the Posidonia Shale in southern Germany, the Jet Rock Beds in the Cleveland Basin of eastern England, and the Schistes Cartons in the Paris and other French basins have been interpreted as the expression of widespread marine anoxic conditions known as the Toarcian Oceanic Anoxic Event (T-OAE; Jenkyns, 1988). The controlling mechanisms and extension of the T-OAE are still debated (see reviews in Caruthers *et al*. 2013, Harazim *et al*. 2013 & Hermoso *et al*. 2013), so are the major environmental disturbances associated with it, e.g. climatic oscillations (van de Schootbrugge *et al*. 2005; Dera *et al*. 2011; Dera & Donnadieu, 2012), carbonate production crisis (Suan *et al*. 2008 and references therein) and disruptions in biogeochemical cycles (Pearce *et al*. 2008; Jenkyns, 2010; Gill *et al*. 2011; Lézin *et al*. 2013). The event took place in a period of severe and protracted biotic crisis that assumed the character of a multi-phased mass extinction affecting both pelagic and benthic marine communities across the Late Pliensbachian and Toarcian (Dera *et al*. 2010; Caruthers *et al*. 2013). The extinction event at the base of the Toarcian is well-documented in the European epicontinental shelf and it has been intensely studied (e.g. Hallam, 1987; Little & Benton, 1995; Harries & Little, 1999; Vörös, 2002; Aberhan & Baumiller, 2003; Cecca & Macchioni, 2004; Wignall *et al*. 2005; Caswell *et al*. 2009; Dera *et al*. 2010). Recently, research efforts have been devoted to investigate the tempo and mode of the post-crisis faunal recovery focusing on entire communities (Danise *et al*. 2013) or on selected groups, such as, for example, benthic foraminifers and calcareous nannofossils (Mailliot *et al*. 2009), brachiopods

(García Joral *et al*. 2011), ammonites (Dera *et al*. 2010; Neige *et al*. 2013), and radiolarians (Goričan *et al*. 2013).

[Figure 1 here]

Studies on the relationship between the changes of gastropod diversity and the Toarcian crisis are very few (e.g. Gründel *et al*. 2011; Monari & Gatto, 2013), the group being mostly considered as a component in analyses of multi-taxa benthic assemblages (Gahr, 2005; Caswell *et al*. 2009; Caswell & Coe, 2012; Danise *et al*. 2013). In this context, the present study provides new data relevant to reconstruct the mode of recovery of this molluscan group based on a thorough systematic analysis of the gastropod fauna from the Upper Pliensbachian to Upper Toarcian succession cropping out in two sections of the Causses region (southern France). The Toarcian species recognized here belong to a faunal stock characteristic of several localities of the European shelf and represent the first repopulation of this Tethyan district after the T-OAE. Until now, knowledge on the Toarcian benthic molluscs from the Causses was limited to the study by Fürsich *et al*. (2001) who recorded few gastropods species. Most taxonomic contributions on Toarcian gastropods concern faunas from northern and southern Germany (Roemer, 1836, 1839; Goldfuss, 1841–44; Quenstedt, 1852, 1856–58, 1884; Oppel, 1854; Denckmann, 1887; Schlosser, 1901; Sieberer, 1907; Brösamlen, 1909; Ernst, 1923; Kuhn, 1935; Walther, 1951; Klöcker, 1966; Gründel, 1999*a*, 1999*b*, 2005, 2007, 2009; Gründel *et al*. 2009; Schulbert & Nützel, 2009, 2013). Studies on other areas of the European epicontinental shelf are much fewer and mostly outdated. They mainly refer to the Paris Basin (Eudes-Deslongchamps, 1842*a*, 1842*b*, 1849; d'Orbigny, 1850, 1851–60; Thevenin, 1908; Cossmann, 1913; Fischer & Weber, 1997), southern France (Dumortier, 1874), England (Moore, 1866; Hudleston, 1889, 1892, 1894, 1895, 1896; Wilson & Crick, 1889; Gründel *et al*. 2011), and Iberian Peninsula (Gahr, 2002). Few other species are recorded from areas that during the Jurassic belonged to the central part of western Tethys, i.e. the central Apennine (central Italy) (Mariotti & Schiavinotto, 1977; Conti & Monari, 1995, 2003), the western Sicily (southern Italy) (Wendt, 1968) and the Transdanubian Central Range (Hungary) (Szábo, 1982, 1995; Gálacz

& Szábo, 2001), and to its north-eastern margin (Pčelincev, 1937). Finally, except for a little Toarcian fauna from Morocco described by Cossmann & Abrard (1921), nothing is known about the gastropods of southern margin of the western Tethys.

Being located at the southern margin of the European shallow-water shelf facing to the central part of western Tethys, the Causses basin might provide useful indications on the relationship between the benthic faunas inhabiting these palaeogeographic sectors during a crucial time of the history of the western Tethys.

2. Geographical and stratigraphical setting

The studied gastropods have been recovered from two sections, Tournadous and Cornus, located about ten kilometres apart in central-southern France (Fig. 1a). These localities have been the subject of several studies mainly on account of their rich cephalopod faunas (e.g. Monestier, 1921*a*, 1921*b*, 1931; Guex, 1972; Meister, 1989; Morard, unpub. Ph.D. Thesis, Université de Lausanne, 2004; Pinard *et al*. 2014). Mailliot *et al*. (2009) analysed in detail the environmental changes at the Pliensbachian–Toarcian boundary in the Tournadous section. Both sections are situated on the southern part of the Causses basin, a small intracratonic basin that during the Jurassic was located along the south-western margin of the European epicontinental shelf (Fig. 1b). The basin was bordered by the Massif Central lands to the North and West, and by the Montagne Noire lands to the South. Communication with adjacent basins was further limited by the Cévennes High, on the eastern side of the basin. Spatial changes in thickness of the different lithostratigraphic units and even hiatuses are suggestive of a marked differential subsidence. Tectonics, stratigraphy and geochemistry aspects of the basin have been thoroughly investigated in a number of studies (e.g. Trümpy, 1983; Graciansky *et al*. 1998; Mailliot *et al*. 2009; Harazim *et al*. 2013; van de Schootbrugge *et al*. 2013).

[Figure 2 here]

The Tournadous section is considered as very proximal (Mailliot *et al*. 2009) and the studied interval (Upper Pliensbachian to Upper Toarcian; Fig. 2) includes three local formations. The Marnes de Villeneuve Fm., at the base of the section, is represented by dark marls. The top of the unit is characterised by a succession of three nodular beds, the uppermost of which indicates the end of the Pliensbachian (Mailliot *et al*. 2009). Fossils are generally well preserved, with cephalopods largely predominant, and gastropods, bivalves (pectinids, plicatulids, nuculids and nuculanids) and small brachiopods rather frequent. The successive Schistes Cartons Fm. is an organic-matter-rich shale occasionally containing silty sediments. At the very base of this formation, Mailliot *et al*. (2009) found a negative $\delta^{13}C$ anomaly that has been tentatively correlated with the well-known negative carbon-isotope excursion (CIE) recorded in numerous sections in NW Europe and elsewhere (Hesselbo *et al*. 2000, 2007; Caswell & Coe, 2012; Hermoso *et al*. 2012; and reference therein). The uppermost unit is represented by the Marnes de Fontaneilles Fm., a monotonous marl succession with rare intercalated carbonate beds that extends up to the Aalenian. Ammonites, belemnites, gastropods and bivalves are frequent. The Cornus section (Fig. 2) has been studied in its well-exposed upper part, equivalent to the Marnes de Fontaneilles Fm. (pars), which has been dated to the Upper Toarcian. Gastropods are frequent, together with more rare bivalves (*Nuculana-Palaeonucula* group).

A detailed chronostratigraphic subdivision has been obtained by the study of the distribution of the ammonites (Pinard *et al*. 2014). All zones have been recognized except the Spinatum Zone (uppermost Pliensbachian) and the Tenuicostatum Zone (lowermost Toarcian). In the Tournadous section a very distinctive calcareous bed (bed number 100 in Pinard *et al*. 2014; Fig. 2) occurs at nearly 20 meters above the base and represents a condensed interval characterised by the occurrence of a time-averaged fossil accumulation dated from the Thouarsense Zone to the base of the Dispansum Zone (Insigne Subzone). The base of the Cornus section contains ammonites from the lower part of the Aalensis Zone (Mactra Subzone), namely *Pleydellia* (*Pleydellia*) *mactra* (Dumortier, 1874), *Pleydellia* (*Pleydellia*) *aalensis* (Zieten, 1832), *Pleydellia* (*Cotteswoldia*)

paucicostata (Buckman, 1904), whereas the top of the section contains ammonites from the upper part of the Aalensis Zone (Fluitans Subzone), such as *Pleydellia* (*Walkericeras*) *fluitans* (Dumortier, 1874) and *Pleydellia* (*Walkericeras*) sp.

Samples for the present study were recovered by surface collection. Although rather abundant, the gastropods do not occur throughout the sections (Fig. 2). They are present in the Margaritatus Zone, Gibbosus Subzone of the Marnes de Villeneuve Fm., mainly preserved as inner moulds. Gastropods have not been found in the Schistes Cartons Fm., although Morard (unpub. Ph.D. Thesis, Université de Lausanne, 2004) reported *Coelodiscus* from nearby localities of Saint-Paul-des-Fonts and Saint-Beaulize. In the Marnes de Fontaneilles Fm., gastropods occur in several levels which are mainly concentrated in the Bifrons Zone, Dispansum Zone, and Aalensis Zone, Mactra Subzone.

3. Systematic palaeontology

The distribution of the species reported below is exclusively based on the synonymy list of the species concerned and, more in detail, on the specimens figured by authors. Most of the morphological terms used in the systematic descriptions are in accordance with Cox (1960). The measurements of the specimens are reported in Table 1 and abbreviations for the dimensions are shown in Figure 3.

[Figure 3 here]

[Table 1 here]

Institutional abbreviations are as follows: UBGD, University of Burgundy, Geology Dijon, France; MNHNL, National Museum of Natural History of Luxembourg, City of Luxembourg, Grand-Duchy of Luxembourg.

Superfamily EOTOMARIOIDEA Wenz, 1938

Family GOSSELETINIDAE Wenz, 1938

Genus *Sisenna* Koken, 1896

Type species. *Pleurotomaria turbinata* Hörnes, 1855. Carnian (Upper Triassic), Northern Calcareous Alps (Austria).

Sisenna canalis (Münster in Goldfuss, 1844)

Figure 4a–l

? 1836 *Trochus helicinoides* Roemer, p. 150, pl. 11, fig. 13.

1844 *Turbo canalis* Münster; in Goldfuss, p. 95, pl. 193, figs 12a, b.

1854 *Turbo canalis* Goldfuss; Oppel, p. 103, pl. 3, figs 20a, b.

1858 *Turbo canalis* Quenstedt, p. 155, pl. 19, figs 32, 33.

1866 *Trochus carinatus* n. s.; Moore, p. 207, pl. 4, figs 24, 25.

1876 *Pleurotomaria helicinoides* Roemer; Tate in Tate & Blake, p. 338, pl. 10, fig. 7.

1884 *Turbo canalis* Quenstedt, p. 427, pl. 201, figs 113, 114.

? 1889 *Pleurotomaria helicinoides* Roemer; Wilson in Wilson & Crick, p. 304, pl. 9, figs 13a, b.

1889 *Pleurotomaria* (*Turbo*) *canalis* Münster; Wilson in Wilson & Crick, p. 304, pl. 9, fig. 14.

1909 *Sisenna canalis* Münster; Brösamlen, p. 200, pl. 17, figs 2a–c.

1936 *Sisenna canalis* Münster; Kuhn, p. 281, pl. 8, figs 8a, b.

1998 *Sisenna canalis* (Münster); Gründel & Nützel, p. 65, pl. 1, figs 3–5.

2008 *Sisenna canalis* (Münster); Nützel, p. 45, pl. 1, fig. 5.

Material. Four specimens: MNHNL QH577, MNHNL QH578, MNHNL QH579, MNHNL QH580, Tournadous, Lower Toarcian, Bifrons Zone.

Dimensions. See Table 1.

Description. Shell very small (height about 5 mm), turbiniform, slightly higher than wide, composed of four teleoconch whorls with a distinctly gradate spire. Height of last whorl about 80% of shell height. Surface of early whorls strongly and evenly convex. Succeeding whorls with shoulder marked by spiral cord and subdividing whorl surface into slightly convex to almost flat ramp and vertical outer face. Fully adult whorls with second obtuse angulation on ramp closer to adapical suture than to shoulder and provided with spiral cord delimiting flat and horizontal subsutural shelf. Part of ramp between angulation and shoulder distinctly concave. Base strongly convex and swollen. Aperture roundedly trapezoidal. Additional spiral thread below shoulder scarcely visible on specimens here described. Base ornamented by regularly spaced spiral threads, seemingly more spaced abaxially. Growth lines prosocline and feebly prosocyrt on ramp, strongly opisthocline and opisthocyrt on outer face, widely prosocyrt on base, becoming slightly opisthocyrt on its axial region.

Remarks. The specimens are mostly preserved as inner moulds with shell remains of the main elements of the external ornament, including traces of the growth lines. According to Brösamlen (1909), *Sisenna canalis* (Münster, 1844) is most probably a junior synonym of *Pleurotomaria helicinoides* Roemer, 1836. In contrast, Wilson & Crick (1889) maintained that *P. helicinoides* is a distinct species. The extremely poor information on this species prevents to establish a safe relationship with *S. canalis*.

Distribution of the species. Upper Pliensbachian, Swabia and Franconia (southern Germany), Yorkshire (north-eastern England); uppermost Pliensbachian to lowermost Toarcian, Leicestershire (central England) and Somersetshire (south-western England); Lower Toarcian, Causses basin (southern France).

[Figure 4 here]

Superfamily PTYCHOMPHALOIDEA Wenz, 1938

Family PTYCHOMPHALIDAE Wenz, 1938

Genus *Angulomphalus* Gründel, 2011

Type-species. *Helicina expansa* Sowerby, 1821. Hettangian–Lower Sinemurian (exact stratigraphical level unknown), Dorset (south-western England).

Angulomphalus expansus (Sowerby, 1821)

Figure 4m–r

1821a *Helicina expansa*; Sowerby, p. 129, pl. 273, figs 1–3.

1821a *Helicina solarioides*; Sowerby, p. 129, pl. 273, fig. 4.

? 1821b *Helicina polita*; Sowerby, p. 153, pl. 285.

? 1831 *Turbo callosus* nobis; Deshayes, p. 189, pl. 4, figs 5, 6.

1832 *Helicina expansa* Sowerby, Zieten, p. 45, pl. 33, figs 5a–c.

? 1837 *Rotella polita* Sow.; Bronn, p. 389, pl. 21, figs 2a–c.

1844 *Rotella expansa* Sow.; Goldfuss, p. 102, pl. 195, figs 8a–c, ?9a–c.

1846 *Helicina polita* Sowerby; Schmidt, p.62, pl. 16, figs 5a–c (as *Helicina expansa*).

1849 *Pleurotomaria suturalis* E.D.; Eudes-Deslongchamps, p. 147, pl. 17, figs 3a–d.

1849 *Cochlicarina expansa* Sowerby; Brown, p. 99, pl. 47, figs 1, 2.

1849 *Cochlicarina solarioides* Sowerby; Brown, p. 99, pl. 47, figs 3, 4.

? 1849 *Cochlicarina polita* Sowerby; Brown, p. 100, pl. 47, figs 5, 6.

1853 *Pleurotomaria expansa* Sow.; Chapuis & Dewalque, p. 97.

1853 *Pleurotomaria expansa* var. *solarioides*; Chapuis & Dewalque, p. 98, pl. 13, figs 3a–d.

1853 *Pleurotomaria expansa* var. *expansa*; Chapuis & Dewalque, p. 99, pl. 13, figs 3e–h.

? 1854 *Pleurotomaria expansa* Sowerby; d'Orbigny, p. 413, pl. 352, figs 1–4.

1858 *Helicina expansa* Sw.; Quenstedt, p. 153, 193, pl. 19, fig. 15, 16, pl. 24, fig. 19.

? 1858 *Helicina expansa plicata*; Quenstedt, p. 193, pl. 23, fig. 34.

1861 *Pleurotomaria expansa* Sow.; Stoliczka, p. 185, pl. 3, figs 16a, b.

1869 *Pleurotomaria expansa* (Sowerby); Dumortier, p. 113, pl. 18, figs 11, 12.

1874 *Pleurotomaria expansa* Sow.; Gemmellaro, p. 114, pl. 13, figs 20a, b.

1876 *Cryptaenia solarioides* Sowerby; Tate in Tate & Blake, p. 335, pl. 10, figs 2a, b.

1876 *Cryptaenia consobrina* spec.nov.; Tate in Tate & Blake, p. 335, pl. 10, figs 22a, b.

1884 *Pleurotomaria expansa* Sow.; Quenstedt, p. 331, pl. 197, figs 54, 55, ?56, 57–59, ?61–66.

? 1884 *Pleurotomaria polita* Sow.; Quenstedt, p. 332, pl. 197, fig. 60.

1888 *Pleurotomaria* (*Cryptaenia*) *expansa* Sowerby; Moberg, p. 60, pl. 2, figs ?32, 33–35.

1894 *Pleurotomaria* (*Cryptaenia*) *expansa* Sow.; Parona, p. 174, pl. 7, figs 7a–c.

1901 *Cryptaenia aperta* Burckhardt; Schlosser, p. 533, pl. 16, figs 20, 24.

1907 *Cryptaenia expansa* Sowerby; Sieberer, p. 25, pl. 1, figs 5a–c.

? 1907 *Cryptaenia nodosa* nov. spec.; Sieberer, p. 26, pl. 1, figs 7a–c.

1908 *Ptychomphalus expansus* (Sow.); Cossmann, p. 64, pl. 2, figs 25–27.

1909 *Cryptaenia expansa* Sow.; Dal Piaz, p. 7, pl. without number, figs 7a–c.

1911 *Cryptaenia expansa* Sow.; Gemmellaro, p. 214, pl. 10, figs 13–16.

1911 *Cryptaenia expansa* var. *subtilistriata*; Gemmellaro, p. 215, pl. 10, figs 17–19.

1936 *Ptychomphalus cirroidens* Young & Bird; Kuhn, p. 280, pl. 8, figs ?2, 7, pl. 9, figs 24a, b, pl. 12, figs 25a, b.

1937 *Cryptaenia expansa* Sow.; Pčelincev, p. 24, pl. 1, fig. 25.

1964 *Ptychomphalus expansus* (Sow.); Sacchi Vialli, p. 3, pl. 1, figs 1a, b.

1966 *Cryptaenia expansa* (Sowerby); Bourrhouilh, p. 43, figs 16a, b.

non 1980 *Ptychomphalus expansus* (Sowerby); Szabó, p. 55, pl. 1, fig. 9 (= *Ptychomphalus kericserensis* Szabó, 2009).

? 1991 *Ptychomphalus* cfr. *expansus* (Sowerby); Conti & Monari, p. 262, pl. 7, fig. 15.

1997 *Ptychomphalus expansus* (Sowerby); Fischer & Weber, p. 160, pl. 26, figs ?1a, b, 2, 3.

1998 *Ptychomphalus expansus* (Sowerby); Gründel & Nützel, p. 66, pl. 1, figs 6–9.

2007 *Ptychomphalus expansus* (Sowerby); Conti *et al*., pl. 12, figs 20a, b.

2008 *Ptychomphalus expansus* (Sowerby); Nützel, p. 45, pl. 1, fig. 5.

2008 *Ptychomphalus expansus* (Sowerby); Schubert *et al*., p. 20, figs 2A–H.

2009 *Ptychomphalus expansus* (Sowerby); Szabó, p. 23, figs 17A–D.

2011*b Angulomphalus expansus* (Sowerby); Gründel, p. 62, pl. 2, figs 4–7.

Material. One specimen: MNHNL QH619, Tournadous, Upper Pliensbachian, Margaritatus Zone, Gibbosus Subzone.

Description. Shell sublenticular-discoidal, composed of six whorls. Apical spire turbiniform, slightly coeloconoid. Teleoconch whorls initially strongly and evenly convex with impressed suture, then progressively less convex, becoming flat or very slightly convex. Selenizone rather prominent and coinciding with peripheral bulge. Selenizone near abapical suture on early whorl, partially or completely covered by suture on adult whorls, except for final half of last whorl. Base only partially preserved, seemingly strongly convex and swollen. Regular pattern of very thin and dense spiral threads on whorl surface including peripheral bulge and selenizone. About twenty threads on surface of last whorl and others visible on preserved parts of base. Selenizone bordered by marginal threads slightly more prominent than those of whorl surface, with central spiral thread coinciding with shallow, obscure angulation of peripheral bulge. Lunulae scarcely visible, seemingly very thin and irregularly sized. Growth lines prosocline and prosocyrt on whorl surface and opisthocline and prosocyrt on peripheral region of base.

Remarks. The specimen is damaged by compaction affecting mainly the base and the last whorl. *Helicina expansa* Sowerby, 1821 has been recently chosen by Gründel (2011*b*) as the type species of his genus *Angulomphalus* Gründel, 2011. The species is among the most frequently recorded Lower Jurassic gastropods. It shows a stratigraphical, palaeogeographic and palaeoenvironmental distribution exceptionally wide for a benthic taxon. Its stratigraphical range includes the interval between the Upper Hettangian–Lower Sinemurian and the Upper Pliensbachian. Caswell *et al*. (2009) listed the species also in the Lower Toarcian (Falciferum Zone) of Yorkshire (north-eastern England). The palaeogeographic distribution encompasses the whole western Tethys, from the European epicontinental shelf to the North-African margin. It is associated with a range of very different facies, occurring in shallow water mixed calcareous-terrigenous deposits, pelagic and carbonate platform sediments.

Most authors highlighted the wide morphological variability of *A. expansus*. Some of them instituted also different varieties (e.g. Chapuis & Dewalque, 1853; Quenstedt, 1858; Gemmellaro, 1911) or recognized different species (Sowerby, 1821; Tate in Tate & Blake, 1876; Schlosser, 1901; Sieberer, 1907; Szabó, 2009). The variability concerns several characters. Variations in the height of the spire and in the convexity of the base give rise to discoidal shells with swollen base to lenticular, symmetrical shells with the base almost as high as the spire. The surface of the last whorl commonly tends to become concave but more rarely it keeps its convexity up to the last peristome. The prominence and shape of the peripheral keel, and consequently of the selenizone, are also variable. In most cases the selenizone is convex and cord-like. In some shells it corresponds to a spiral groove edged by sharp threads within a somewhat prominent peripheral keel. The subsutural bulge is variably marked, reflecting the degree of overlap of the suture on the periphery of the previous whorl, and the prominence of the periphery itself. It can be smooth or provided with nodes that commonly disappear in the fully adult whorls. These nodes vary from evenly spaced and sized tubercles to very irregularly distributed and sized subsutural wrinkles. The basal callus filling the

umbilicus varies from thick and swollen to relatively thin and flat. In the latter case, it often draws an axial depression which reflects the presence of a wide umbilicus. Finally, the shell can be smooth or ornamented by sharp and dense spiral lines or threads.

Although several authors (e.g. Schubert *et al*. 2008; Szabó, 2009) did not exclude the possibility that *A. expansus* represents different species and suggested its revision, the analysis of the available literature does not evidence clear discontinuities, mainly because the variable morphological characters are largely independent to each other. The only useful macroscopical tract could be represented by the presence/absence of subsutural nodes. Nodes were described and well illustrated by numerous authors (Deshayes, 1831; Bronn, 1837; Goldfuss, 1844; d'Orbigny, 1854; Quenstedt, 1858, 1884; Moberg, 1888; Sieberer, 1907; Kuhn, 1936; Fischer & Weber, 1997) and their presence was used by Quenstedt to distinguish the variety *plicata*. Sieberer (1907) erected a new species naming it as *Cryptaenia nodosa* Sieberer, 1907. Gründel (2011*b*) synonymised these taxa under the name *Angulomphalus plicatus* (Quenstedt, 1858). Also Szabó (2009) maintained that the presence of nodes, together with the shape of the selenizone, could be useful to distinguish distinct species. However, Fischer & Weber (1997) revising the rather rich material of d'Orbigny's collection found a continuity between smooth and nodose shells of *A. expansus*. As a matter of fact, nodes are the only distinctive character in otherwise indistinguishable shells. The question remains open and the extensive synonymy list compiled here represents a contribution for a future review.

Distribution of the species. Undifferentiated Hettangian–Lower Sinemurian, Dorset (south-western England); uppermost Hettangian to lowermost Sinemurian, Yorkshire (north-eastern England); undifferentiated Hettangian–Sinemurian southern Belgium; undifferentiated Sinemurian, north-western Lombardian Basin (northern Italy); undifferentiated Sinemurian–Pliensbachian, south-eastern Scania (southernmost Sweden); Upper Sinemurian, Caucasus (southern Russia), Northern Calcareous Alps (Austria) and eastern High Atlas (Morocco); undifferentiated Pliensbachian, Trento Plateau (Southern Alps, Italy); Lower Pliensbachian, Vendée (western France), Saone-et-Loire

(eastern France), eastern Sicily (Calabrian Arc, southern Italy) and Middle Atlas (Morocco); Upper Pliensbachian, Yorkshire (north-eastern England), Franconia and Swabia (southern Germany), Herford and Lower Saxony (northern Germany), Calvados (northern France), Causses basin (southern France); Upper? Pliensbachian, Sicani Mountains (western Sicily).

Superfamily PLEUROTOMARIOIDEA Swainson, 1840

Family PLEUROTOMARIIDAE Swainson, 1840

Genus *Pleurotomaria* Defrance, 1826

Type species. *Trochus anglicus* Sowerby, 1818. Upper Pliensbachian, Somerset (south-western England).

Pleurotomaria amalthei Quenstedt, 1858

Figure 5a–d

1844 *Pleurotomaria anglica* (Sowerby); Goldfuss, p. 69 pl. 184, fig. 8.

1854 *Pleurotomaria anglica* Goldfuss; Oppel, p. 99, pl. 3, fig. 15.

1858 *Pleurotomaria amalthei* Quenstedt, p. 191, pl. 23, figs 31, 32.

1884 *Pleurotomaria amalthei* Quenstedt; Quenstedt, p. 352, pl. 198, figs 48–50.

1907 *Pleurotomaria amalthei* Quenstedt; Sieberer, p. 17, text-fig. 2, pl. 2, fig. 1.

1907 *Pleurotomaria amalthei* var. *elegans* Sieberer; p. 19, pl. 1, fig. 4.

1936 *Pleurotomaria amalthei* Quenstedt; Kuhn, p. 273, pl. 8, fig. 13.

1998 *Pleurotomaria amalthei* Quenstedt; Gründel & Nützel, p. 64, pl. 1, figs 1, 2.

2008 *Pleurotomaria amalthei* Quenstedt; Nützel, p. 41, pl. 1, figs 1, 2.

2010 *Pleurotomaria* sp.; Lindström & Peel, p. 542, figs 1C, F.

Material. One specimen: UBGD 278805, Tournadous, Upper Pliensbachian, Margaritatus Zone, Gibbosus Subzone.

Dimensions. See Table 1.

Description. Shell trochiform and gradate, with rather high whorls. First teleoconch whorls strongly and evenly convex with impressed sutures. Fully adult whorls bearing quite obtuse angulation slightly above mid-line. Ramp quite inclined and slightly convex to almost flat. Outer face feebly convex and wider than ramp. Selenizone flat, slightly below the shoulder on early whorls, slightly above the middle of outer face on adult whorls. Selenizone initially very wide, covering slightly less than half of outer face, then narrowing to slightly less than one fourth of outer face. Periphery subangulated and with suture running on it. Base of last preserved whorl rather flat and with moderately wide umbilicus. Surface of teleoconch ornamented by sharp and densely packed growth threads, making rough the shell surface, gently waving the spiral ornament and forming granulations at intersection points. Ramp ornamented initially by one median spiral thread, then by up to three widely spaced and sharp threads. Shoulder bearing sharp and strong spiral cord with slightly pointed and widely spaced, spirally elongated nodes. Nodes more prominent on adult shell, about twenty on penultimate whorl. Outer face of early whorls bearing two sharp spiral threads delimiting selenizone and an equally sized spiral thread running between selenizone and abapical suture. Secondary spiral thread appearing during growth above and below selenizone. Suprasutural spiral thread with numerous, axially elongate nodes, less spaced than those of shoulder and forming short, shallow collabral rib-like swellings on periphery of last whorl. Selenizone ornamented by sharp, densely and evenly spaced lunulae and by median lira on adult whorls. On last whorls, median lira stronger than spiral threads delimiting selenizone. Peripheral band of base ornamented by strong spiral threads waved by collabral swellings. Growth lines slightly prosocline and feebly prosocyrt on ramp, more strongly prosocyrt on shoulder above selenizone, evenly opisthocyrt on

selenizone, orthocline or feebly opisthocline and distinctly prosocyrt below selenizone and on peripheral band.

Remarks. Although poorly preserved, the specimen shows the shell shape and ornament characters typical of *Pleurotomaria amalthei* Quenstedt, 1858. These are the somewhat narrow and strongly sloping ramp, the rather wide selenizone, and the spiral cord on shoulder more prominent than the other spiral elements of the shell. The specimen from the Upper Pliensbachian of Dorset (south-western England) illustrated by Lindström & Peel (2010, figs 1C, F) as *Pleurotomaria* sp. is here considered as belonging to *P. amalthei* although it shows less prominent peripheral nodes.

Distribution of the species. Upper Pliensbachian, Swabia and Franconia (southern Germany), Dorset (south-western England), and Causses basin (southern France).

[Figure 5 here]

Pleurotomaria escheri Goldfuss, 1844

Figure 5e–h

1844 *Pleurotomaria Escheri* nobis; Goldfuss, p. 70, pl. 184, figs 9a, b.

? 1844 *Pleurotomaria tuberculato-costata* Münster; Münster in Goldfuss, p. 70, pl. 184, fig. 10.

1844 *Pleurotomaria Studeri* Münster; Münster in Goldfuss, p. 70, pl. 184, fig. 11.

1907 *Pleurotomaria Escheri* Münster; Sieberer, p. 20, pl. 1, figs 11a, b.

1935 *Pleurotomaria studeri* Münster; Kuhn, p. 128, pl. 9, fig. 19, pl. 10, figs 6, 34.

non 1964 *Pleurotomaria escheri* Goldfuss; Sacchi Vialli, p. 5, pl. 1 figs 5, 6.

2009 *Pleurotomaria escheri* Goldfuss; Schulbert & Nützel, p. 477, figs 2A–C.

2013 *Pleurotomaria escheri* Goldfuss; Schulbert & Nützel, p. 728, figs 5A–C.

Material. One specimen: MNHNL QH581, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone.

Dimensions. See Table 1.

Description. Shell gradate, with somewhat high spire composed of strongly convex whorls separated by impressed sutures. Whorls subangulated by rounded, nodose shoulder. Ramp slightly inclined and rather narrow, about one third of outer face. Outer face slightly and evenly convex. Selenizone flat, rather wide, placed at middle of outer face and delimited by two sharp spiral threads. Base and aperture not preserved. Ornament composed of spiral threads and collabral ribs. Ramp of last preserved whorls ornamented by four, strong and evenly spaced spiral threads and about sixteen, strong and rounded collabral ribs forming weakly swollen and barely defined nodes on shoulder. Two stronger spiral threads running on shoulder. Periphery seemingly marked by a prominent and swollen bulge, limited below by suture. Selenizone with median lira and numerous, sharp and regularly spaced lunulae. Growth lines forming thin, sharp and evenly spaced threads on early shell, changing to packed and sharp striae on fully adult shell. Growth lines prosocline and feebly prosocyrt on ramp, opisthocline between selenizone and abapical suture.

Remarks. Although poorly preserved, the specimen shows the distinctive characters of *Pleurotomaria escheri* Goldfuss, 1844. They consist of a somewhat high, gradate early shell with strongly convex whorls, a rather narrow ramp ornamented by widely spaced, prominent and rounded ribs, barely defined nodes at the shoulder formed by a weak swelling of the collabral ribs, and a rather wide selenizone. Due to the poor preservation, the peripheral bulge, which is another distinctive character of the species, is scarcely visible in the specimen here described. The type figured by Goldfuss (1844) differs only in a slightly higher number of both collabral ribs and spiral threads on the ramp. *Pleurotomaria tuberculatocostata* Münster in Goldfuss 1844, a poorly

documented species from the Lower Pliensbachian of Franconia (southern Germany) (Schlosser, 1901; Trauth, 1908), is seemingly distinguished from *P. escheri* only by having a less prominent peripheral bulge.

Distribution of the species. Upper Pliensbachian, Swabia (southern Germany); Upper Toarcian, Causses basin (southern France); Upper Toarcian and Lower Aalenian, Franconia (southern Germany).

Genus *Bathrotomaria* Cox, 1956

Type species. *Trochus reticulatus* Sowerby, 1821. Kimmeridgian, Dorset (south-western England).

Bathrotomaria kronzwilmesorum sp. nov.

Figure 5i–q

Etymology. From Guy Kronz and his wife Liette Wilmes, scientific collaborators of the National Museum of Natural History of Luxembourg, who collected the material.

Holotype. MNHNL QH620 (Fig. 5i–q).

Type locality. Tournadous, Causses region (southern France).

Type level. Marnes de Fontaneilles Fm, Early Toarcian, Bifrons Zone, Bifrons Subzone.

Material. A single specimen (holotype), MNHNL QH620.

Dimensions. See Table 1.

Diagnosis. Turbiniform earliest teleoconch with strongly convex whorls and prominent suprasutural cord. Distinctly gradate fully adult shell with whorls having a convex ramp and concave outer face. Ramp twice the width of the outer face. Selenizone of early teleoconch whorls wide, concave to flat and adjacent to the suprasutural cord. Selenizone of fully adult whorls corresponding to the angulation of the whorl surface and to a wide, very prominent spiral keel ornamented by thin spiral threads. Periphery of the fully adult shell marked by a swollen spiral bulge. Base anomphalous, with a deep axial cavity encircled by a sharp spiral keel. Early teleoconch ornamented by a sharp and regular network of spiral threads and collabral riblets. Fully adult whorls and base ornamented by marked spiral threads.

Description. Shell medium-sized, trochiform, composed of about eight whorls. Earliest spire turbiniform and slightly cyrtoconoid. Fully adult shell gradate and weakly coeloconoid. Protoconch with slightly depressed nucleus and composed of one and half, rounded and seemingly smooth volutions. First three teleoconch whorls strongly convex with somewhat impressed suture and cord-like periphery. Succeeding whorl angulated slightly above peripheral cord. Angulation more and more distinct during growth, shifting slightly abapically, and separating wide, oblique and convex ramp from narrow, concave and almost vertical outer face. Ramp about twice width of outer face. Periphery quite prominent and bulged, partially covered by suture. Selenizone wide, concave and adjacent to peripheral cord on first teleoconch whorl, flat on subsequent whorl. Selenizone on adult shell corresponding to shoulder of whorl surface, forming wide, rounded and quite prominent spiral cord. Base low, with slightly convex surface, anomphalous and with deep axial cavity (pseudoumbilicus). Aperture subtrapezoidal with discontinuous peristome on parietal lip. Inner lip very stout, oblique and gently arched, reinforced by slightly outward reflected callus. Parietal lip covered by thin shell layer in continuity with columellar callus and extended to sutural corner. Outer

lip sharp. Slit seemingly extended about one fourth of last whorl. Ornament of early teleoconch consisting of a regular network of equally sharp spiral threads and collabral riblets with small granules at intersection points. Spiral threads increasing in number during growth; three to four on second teleoconch whorl and about eight on ramp of antepenultimate whorl. Spiral ornament becoming progressively dominant on last two whorls; collabral riblets persisting only as punctuations within thin interspaces of spiral threads. Last whorl ornamented by about fifteen spiral threads on ramp and half a dozen on outer face. Few spiral threads on peripheral bulge, wider than those of outer face. Selenizone lacking spiral ornament at beginning of teleoconch and with sharp and evenly spaced lunulae. Selenizone having one median lira on second whorl. Lunule fading during growth. Spiral threads on selenizone increasing in number up to half a dozen on last whorl. Base sculptured by spiral threads progressively thicker towards axial region, some of them also duplicated. Axial cavity delimited by sharp and prominent spiral keel. Growth lines prosocline and widely prosocyrt on ramp, opisthocline and prosocyrt on outer face and on peripheral bulge, forming irregular wrinkles and distinctly sinuous on base, i.e. opisthocyrt on its abaxial half and prosocyrt on adaxial one.

Remarks. The single specimen is in a very good state of preservation. *Bathrotomaria kronzwilmesorum* sp. nov. is reminiscent of *Bathrotomaria*? *turgidula* (Eudes-Deslongchamps, 1849) (p. 125, pl. 10, fig. 4; d'Orbigny, 1855, p. 427, pl. 356, fig. 4; Fischer & Weber, 1997, p. 163) from the Upper Pliensbachian deposits of Calvados (northern France), in having a wide and prominent selenizone, a wide and convex ramp, and a similar ornament pattern. The species from Calvados is poorly known. It was instituted as a variety of *Pleurotomaria hyphanta* Eudes-Deslongchamps, 1849 and subsequently raised to species rank by d'Orbigny (1850). According to Fischer & Weber (1997) the type material is missing and the species has not been recorded since d'Orbigny (1855). The original illustration shows a fragmentary specimen preserving only the last whorl. It differs from *B. kronzwilmesorum* in having a convex outer face, a more convex ramp, a

roundly angulated periphery lacking spiral bulge, and a more swollen base. Moreover, *B.*? *turgidula* has a small umbilicus (Eudes-Deslongchamps, 1849; d'Orbigny, 1855) whereas *B. kronzwilmesorum* is anomphalous.

Bathrotomaria gaudryana (d'Orbigny, 1855) (p. 447, pl. 364, figs 11, 12; Fischer & Weber, 1997, p. 169, pl. 33, figs 1a–c) from Early Toarcian of Rhône Basin (southern France) differs from *B. kronzwilmesorum* in having a higher and narrowly phaneromphalous shell, with a flat outer face and ramp. Moreover, it shows a finer ornament and a thinner selenizone which is also higher on the whorl surface. *Pleurotomaria subtilis* Münster in Goldfuss, 1844 (p. 71, pl. 185, fig. 4; Khun 1935, p. 129, pl. 9, fig. 27, pl. 10, figs 15, 41) from Lower Aalenian of Franconia (souther Germany) differs from *B. kronzwilmesorum* in having a wider apical angle and the outer face wider than the ramp. Moreover, the outer face is almost flat and oblique, and the selenizone is flush, with a median lira and runs on the outer face. The specimen from Lower Aalenian of Franconia described by Schulbert & Nützel (2013, p. 726, figs 4A-D) as *Laevitomaria*? cf. *subtilis* (Münster in Goldfuss, 1844) is distinguished from the species here described by having a flush selenizone ornamented by two spiral threads in the fully adult shell, a slightly less gradate shell, and higher and less convex early teleoconch whorls.

Distribution of the species. Lower Toarcian, Causses basin (southern France).

[Figure 6 here]

Superfamily TROCHOIDEA Rafinesque, 1815

Family NODODELPHINULIDAE Cox, 1960

Genus *Costatrochus* Gründel, 2009

Type species. *Turbo subduplicatus* d’Orbigny, 1850. Lower Jurassic, Germany, stratigraphical level and locality uncertain (Gründel 2009).

Costatrochus subduplicatus (d'Orbigny, 1850)

Figure 6a–w

1836 *Trochus duplicatus* Sow.; Bronn, 385, pl. 21, figs 3a, b.

1844 *Turbo duplicatus* Sow.; Goldfuss, p. 95, pl. 179, figs 2a–c.

1844 *Turbo plicatus* nobis; Goldfuss, p. 96, pl. 179, fig. 3.

1850 *Turbo subduplicatus* d’Orb.; d'Orbigny, p. 248.

1850 *Turbo palinurus* d'Orb.; d’Orbigny, p. 248.

1853 *Turbo subduplicatus* d’Orb.; d’Orbigny, p. 339, pl. 329, figs 1–6.

1858 *Trochus duplicatus* Goldfuss; Quenstedt, p. 314, pl. 43, figs 18, 19.

1884 *Trochus duplicatus* Sowerby; Quenstedt, p. 428, pl. 201, figs 120–122.

1894 *Trochus subduplicatus*, d’Orbigny; Hudleston, p. 375, pl. 31, figs 13, 14.

1909 *Trochus subduplicatus* Orbigny; Brösamlen, p. 211, pl. 17, figs 23–24, pl. 18, fig. 1.

1935 *Trochus subduplicatus* d’Orb.; Kuhn, p. 133, pl. 9, fig. 35, pl. 10, fig. 1.

1935 *Trochus subduplicatus* d’Orb. var. *münsteriana* nov. var.; Kuhn, p. 133, pl. 10, fig. 2.

1966 *Amphitrochus subduplicatus* (d’Orbigny); Klöcker, p. 242, fig. 9.

1997 *Amberleya subduplicata* (d'Orbigny); Fischer & Weber, p. 135, pl. 21, figs 22, 23.

2001 *Amphitrochus* (*Amphitrochus*) *subduplicatus* (d’Orbigny); Fürsich *et al*., p. 176, fig. 4C.

2009 *Amphitrochus subduplicatus* (d’Orbigny); Schulbert & Nützel, p. 481, figs 5A–D.

2009 *Costatrochus subduplicatus* var. *subduplicatus* (d’Orbigny); Gründel, p. 208, figs 2D, E–M, 4A–E, H, I.

2009 *Costatrochus subduplicatus* var. *palinurus* (d’Orbigny); Gründel, p. 211, fig. 2C, figs 3A–M, 4F, G.

2013 *Costatrochus subduplicatus* (d’Orbigny); Schulbert & Nützel, p. 735, figs 10A–D.

Material. 179 specimens: MNHNL QH582, MNHNL QH583, MNHNL QH584, MNHNL QH585, MNHNL QH586, MNHNL QH587, MNHNL QH588, MNHNL QH589, MNHNL QH590, MNHNL QH591 (87 specimens), UBGD 278806 (10 specimens), UBGD 278807 (72 specimens), UBGD 278808, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone. 23 specimens: MNHNL QH592, Cornus, Upper Toarcian, Aalensis Zone, Lugdunensis Subzone. 7 specimens; UBGD 278809, Cornus, Upper Toarcian, upper part of Aalensis Zone. 6 specimens: MNHNL QH593 (2 specimens), UBGD 278810 (2 specimens), UBGD 278815, UBGD 278816, Tournadous, Lower Toarcian, Bifrons Zone, Bifrons Subzone. 4 specimens: MNHNL QH617, MNHNL QH618, UBGD 278811 (2 specimens), Tournadous, Lower Toarcian, Bifrons Zone. 4 specimens: UBGD 278812, Tournadous, transition Bifrons Zone to Variabilis Zone. 4 specimens: MNHNL QH594, UBGD 278813 (3 specimens), Tournadous, Upper Toarcian, condensed Thouarsense Zone to Dispansum Zone, Insigne Subzone. 3 specimens: UBGD 278814 (2 specimens), UBGD 278842, Tournadous, Upper Toarcian, Dispansum Zone, Insigne Subzone. 4 specimens: UBGD 278817, Tournadous, Upper Toarcian, Pseudoradiosa Zone. 16 specimens: MNHNL QH595, MNHNL QH596, MNHNL QH597, MNHNL QH598 (10 specimens), UBGD 278818 (3 specimens), Tournadous, Upper Toarcian, Aalensis Zone, Mactra Subzone.

Dimensions. See Table 1.

Description. Shell trochiform, acute, with conical to slightly coeloconoid outline, composed of about eight moderately low whorls. Whorls width more than three times whorls height. Height of last whorl slightly more than half of shell height. Protoconch obtuse and seemingly depressed. Early teleoconch whorls distinctly concave, with strong peripheral bulge just above abapical suture. Adult whorls concave adapically, flat or feebly convex abapically. Base convex, swollen and anomphalous, with axial region narrowly depressed beside inner lip. Aperture subcircular, lying almost in one plane and moderately prosocline, discontinuous on parietal lip. Outer lip simple,

angulated at periphery and evenly convex in basal part. Parietal lip covered by thin inductura. Columella stout. Inner lip with somewhat broad, comma-shaped and excavated outer columellar face limited by sharp outer rim. Callus covering partially or completely outer columellar face in fully adult shells. Two nodose spiral cords on first teleoconch whorls: first cord with small, collabrally elongate nodes just below adapical suture; second cord sharp, thicker and more prominent with spiny, very prominent nodes just above abapical suture. Whorl surface covered by about ten fine, closely set spiral threads and by strongly prosocline, rather robust collabral ribs (20-25 per whorl) of constant thickness and regularly separated by slightly wider interspaces. Collabral ribs and spiral threads disappearing almost completely on adult whorls. Adapical cord changing into slightly elevated subsutural band on last whorls. Abapical cord changing into distinctly prominent peripheral bulge sculptured with rather strong and short collabral ribs crossed by 5-8 sharp and thin spiral threads with little nodes at intersections. Base with spiral threads of irregular strength and irregularly spaced, usually more marked abaxially. More or less prominent, sharp collabral wrinkles on axial region of base. Growth lines rather distinct, prosocyrt on subsutural band, then prosocline and gently opisthocyrt on whorl surface, reverting to prosocyrt on peripheral bulge. Growth lines sinuous on base, widely opisthocyrt abaxially and prosocyrt adaxially.

Remarks. Costatrochus subduplicatus (d'Orbigny, 1850) has been widely reported and described, as evidenced by the synonymy list. Most authors remarked its high variability and Gründel (2009) provided a detailed treatment to which the reader is referred. The material here described is more variable than that recorded by Gründel (2009), especially in the spire angle. In the specimens with a wider spire angle, some sculptural elements, such as nodes of the cords and collabral wrinkles of the axial region of the base, are generally more pronounced.

Distribution of the species. Lower Toarcian, Burgundy (eastern France); Lower and Upper Toarcian, Causses basin (southern France); Upper Toarcian, Gloucestershire and Somersetshire (south-

western England); Upper Toarcian and Lower Aalenian, Lorraine and Alsace (eastern France), Swabia and Franconia (southern Germany).

Superfamily EUCYCLOIDEA Koken, 1896

Family EUCYCLIDAE Koken, 1896

Genus *Eucyclus* J. A. Eudes-Deslongchamps, 1860

Type species. *Eucyclus obeliscus* J.A. Eudes-Deslongchamps, 1860. Pliensbachian, Calvados (northern France).

Eucyclus escheri (Münster in Goldfuss, 1844)

Figure 7a–e

1844 *Turbo escheri* Münster; Goldfuss, p. 96, pl. 193, fig. 14.

1909 *Eucyclus escheri* Münster; Brösamlen, p. 259, pl. 20, fig. 11

1936 *Eucyclus escheri* Münster; Kuhn p. 290, pl. 9, fig. 25.

2008 *Eucyclus* ?*escheri* (Münster); Nützel, p. 45, pl. 1, fig. 7.

Material. Two specimens: MNHNL QH599, MNHNL QH600, Tournadous, Lower Toarcian, Bifrons Zone.

Description. Shell moderately high-turbiniform. Early spire with slightly cyrtoconoid outline becoming pagodiform during growth. Periphery marked by sharp angulation running close to abapical suture on early teleoconch whorls and delimiting narrow suprasutural band. Ramp convex above periphery. Suprasutural band becoming progressively wider and forming outer face inclined in direction opposite to that of ramp. Ramp width about three times width of outer face. Lower edge

of outer face marked by obtuse angulation less sharp than peripheral one and just hidden by suture. Ramp wide, feebly convex to almost flat and strongly sloping on fully adult whorls. Base strongly convex and anomphalous. Aperture elliptical and angulated at end of periphery on outer lip. Inner lip almost straight, forming rounded angle at junction with basal lip. Ornament mainly of densely and minutely nodose spiral cords. Cord on periphery more prominent and provided with larger nodes. Ramp ornamented by two, then three evenly sized and equally spaced, nodose spiral cords. Obtuse angulation at lower edge of outer face also marked by nodose cord less prominent than peripheral one. Slightly nodose spiral thread seemingly present at middle of outer face. Base ornament by about ten, evenly sized and equally spaced, obscurely nodose spiral threads. Growth lines scarcely visible, seemingly prosocline and straight on whorl surface and widely prosocyrt on base.

Remarks. The shell wall of the specimens here described has been strongly altered by the recrystallization, which exalted the most prominent features of the ornament, e.g. the primary spiral carinae and their nodes, and almost obliterated the finest sculptural elements. In spite of this, many of the distinctive characters of *Eucyclus escheri* (Münster in Goldfuss, 1844) are still recognizable. They include the subpagodiform shell with conical early spire, the angulated periphery marked by a nodose carina running just besides the suture in the early spire and progressively farther from the suture in the fully adult shell, the almost flat and wide ramp ornamented by two to three nodose spiral cords, and the base bearing numerous barely nodose spiral cords. The species is described by Münster (in Goldfuss 1844) as having secondary spiral threads alternating to nodose spiral carinae. In the specimens here described the secondary ornament is not visible, most probably due to the poor preservation.

A number of coeval species shows close affinities with *E. escheri*. *Eucyclus dunkeri* (Goldfuss, 1844) (p. 95, pl. 193, figs 11a, b; Kuhn, 1936, p. 289, pl. 9, figs 30, 31; Gründel & Nützel, 1998, p. 68, pl. 2, figs 6, 7; Nützel & Kiessling, 1997, p. 389, pl. 34, figs 1–4, as *Eucyclus*

elegans), from the Upper Pliensbachian of Franconia (southern Germany) differs from *E. escheri* in having a turbiniform shape due to more convex whorls. The adult whorls are ornamented by sharper, acute spiral carinae and by a dense pattern of thin growth riblets which form smaller and more packed nodes at the intersection points. *Eucyclus gaudryanus* (d'Orbigny, 1853) (p. 268, pl. 311, figs 4–7; Fischer & Weber, 1997, p. 105), from the Pliensbachian of Calvados (southern France), is similar in the shell shape and ornament pattern, but the shell is almost twice as big and the carinate obtuse angulation below the peripheral keel is much less distinct. *Eucyclus generalis* (Münster in Goldfuss, 1844) (p. 98, pl. 194, fig. 4; Kuhn, 1936, p. 291, pl. 9, fig. 50, pl. 12, fig. 23) a species from the Pliensbachian of Franconia (southern Germany), *Turbo metis* Münster in Goldfuss, 1844 (p. 96, pl. 193, figs 13a, b), and *Trochus cincinnus* Moore 1866 (p. 207, pl. 4, figs 28, 29) from the Middle Lias of Somersetshire (south-western England) might fall into the variability of *E. escheri*. The poor available information on these species prevents more detailed comparisons.

Distribution of the species. Lower and Upper Pliensbachian, Franconia (southern Germany); Lower Toarcian, Causses basin (southern France); Lower Aalenian, Swabia (southern Germany).

Eucyclus elegans (Münster in Goldfuss, 1844)

Figure 7f–h

1844 *Turbo elegans* Münster; Münster in Goldfuss, p. 94, pl. 193, figs 10a, b.

1844 *Turbo venustus* Münster; Münster in Goldfuss, p. 94, pl. 193, figs 9a, b.

non 1876 *Eucyclus elegans* Münster; Tate in Tate & Blake, p. 346, pl. 9, fig. 30.

1909 *Eucyclus elegans* Münster; Brösamlen, p. 256, pl. 20, figs 7a, b.

1936 *Eucyclus elegans* Münster; Kuhn, p. 288, pl. 9, fig. 32.

1936 *Eucyclus venustus* Münster; Kuhn, p. 288, pl. 9, figs 19, 20, 22, 33.

non 1997 *Eucyclus elegans* (Münster); Nützel & Kiessling, p. 389, pl. 34, figs 1–4.

1998 *Eucyclus elegans* (Münster); Gründel & Nützel, p. 67, pl. 2, figs 4, 5.

2008 *Eucycloscala elegans* (Münster); Schubert *et al*., p. 22, figs 3J, K.

2008 *Eucyclus elegans* (Münster); Nützel, p. 45, pl. 1, fig. 6.

Material. Two specimens: MNHNL QH601, MNHNL QH602, Tournadous, Lower Toarcian, Bifrons Zone.

Dimensions. See Table 1.

Description. Shell moderately high-turbiniform and pagodiform. About four teleoconch whorls observable, well rounded, slightly angulated at periphery and separated by impressed sutures. Periphery below middle of whorl surface. Base evenly convex and passing smoothly to whorl surface. Aperture elliptical and roundedly angulated at termination of periphery on outer lip. Ornament mainly of spiral elements. Peripheral subangulation marked by spiral thread. Surface of whorl ornamented by two widely and evenly spaced spiral threads above periphery and by one spiral thread below periphery next to suture. Thinner spiral thread visible on last whorl between peripheral and suprasutural threads. Base ornamented by half a dozen thinner and slightly less spaced spiral threads. Fine collabral threads forming granules at intersection with spiral ornament. Growth lines prosocline on spire and widely prosocyrt on base.

Remarks. The material is composed of inner moulds preserving traces of the shell that shows the ornament and the growth lines. The moderately high turbiniform shell, the strongly convex whorls, the roundedly angulated periphery and the ornament pattern correspond well to those of *Eucyclus elegans* (Münster in Goldfuss, 1844). The specimen figured by Tate (in Tate & Blake 1876) as *E. elegans*, from the latest Hettangian to earliest Sinemurian of Yorkshire (south-eastern England), has

a more acute, slender spire, and less convex whorls with a more angulated periphery. The periphery is lower on the whorl surface and the spiral ornament is stronger.

The species was recorded by previous authors in Upper Pliensbachian sediments. The material here described extends its stratigraphical distribution to the Lower Toarcian.

Distribution of the species. Upper Pliensbachian, Franconia and Swabia (southern Germany), Herford (north-western Germany); Lower Toarcian, Causses basin (southern France).

[Figure 7 here]

Genus *Ooliticia* Cossmann, 1893

Type species. *Turbo phillipsi* Morris & Lycett, 1851. Bathonian, Yorkshire (north-eastern England).

Ooliticia? cf. *cyclostoma* (Benz in Zieten, 1832)

Figure 7i–k

cf. 1832 *Turbo cyclostoma* Benz; Benz in Zieten, p. 45, pl. 33 figs 4a, b.

cf. 1852 *Turbo cyclostoma* Ziet.; Quenstedt, p. 420, pl. 33, fig. 35.

cf. 1857 *Turbo cyclostoma* Zieten; Dumortier, p. 213, pl. 10, figs 2, 2a, b.

? 1887 *Amberleya callipyge*, spec. nov.; Wilson, p. 8, pl. 5, figs 7, 7a.

cf. 1908 *Littorina*? *chartroni* nov. sp.; Cossmann, p. 56, pl. 2, figs 5, 6.

cf. 1909 *Turbo cyclostoma* Benz; Brösamlen, p. 230, pl. 19, fig. 2 (*cum syn*.).

cf. 1916 *Ooliticia chartroni* (Cossmann); Cossmann: 126, pl. 4, figs 1, 2.

cf. 1936 *Turbo cyclostoma* Benz; Kuhn, p. 286, pl. 8, fig. 9.

cf. 2008 *Ooliticia*? *cyclostoma* (Benz); Schubert *et al*., p. 23, figs 3L, M, 4A–C.

cf. 2011 *Ooliticia*? *cyclostoma* (Benz); Gründel *et al*., p. 489, figs 6G, H.

Material. One specimen: UBGD 278819, Tournadous, Upper Pliensbachian, Margaritatus Zone, Gibbosus Subzone.

Dimensions. See Table 1.

Description. Shell turbiniform, presumably composed of half a dozen whorls. Height of last whorl about three fourths of shell height. Whorls strongly convex and with rounded periphery above suture, approximately at lower third of whorl surface. Base convex and passing smoothly to whorl surface. Aperture drop-shaped, pointed at sutural corner. Inner lip slightly arched and elongated downwards at junction with basal lip, perhaps forming a short outlet. Spiral ornament of about seven, evenly spaced cord-like threads. Lowermost thread thicker and more prominent coinciding with suture. Spiral ornament superimposed to weak, slightly prosocline and feebly prosocyrt collabral wrinkles somewhat irregular in size and distribution. Two spiral threads visible on peripheral band of base.

Remarks. The material is represented by an inner mould reproducing the main characters of the ornament. These characters and the shape of the shell are comparable with those of *Ooliticia*? *cyclostoma* (Benz, 1832). The species and its genus position have been discussed by Schubert *et al*. (2008), to which paper reference may be made for details. The analysis of the past literature reveals a somewhat high variation of the height of the spire and of the density and strength of the spiral ornament. The specimen here described approaches better those having a low spire and less dense spiral ornament, such as the shells figured by Quenstedt (1856, pl. 19, fig. 27 right side), Tate (in Tate & Blake, 1876, pl. 9, fig. 20), and Schubert *et al*. (2008, figs 4A, B).

The relationship of synonymy between *Turbo cyclostoma* and *Phasianella paludinaeformis* Schübler in Zieten, 1832 (p. 40, pl. 30, figs 12, 13) has been underlined by several authors

(Quenstedt, 1843, 1858, 1884; Oppel, 1856–58; Brösamlen, 1909). Both species were introduced in the same year and in the same monograph. The first reviser of the species was Quenstedt (1843 p. 551) who explicitly mentioned the synonymy and fixed the name *cyclostoma* (ICZN 1999, Art. 24.2).

In agreement with Gründel *et al*. (2011), *Ooliticia chartroni* (Cossmann 1908) from the Upper Pliensbachian of Vendée (western France) is synonymous of *O*.? *cyclostoma*. *Amberleya callipyge* Wilson, 1887 from the Upper Pliensbachian beds of the Northamptonshire (central England) is also placed in synonymy with Benz's species by Gründel *et al*. (2011), but it shows a lower spire and a flatter whorl surface.

Distribution of the species. *Ooliticia*? *cyclostoma* occurs in Upper Pliensbachian deposits of Franconia and Swabia (southern Germany), Herford (north-western Germany), Yorkshire (north-eastern England), Vendée (western France), Saône-et-Loire (eastern France), southern Belgium and possibly Causses basin (southern France).

Genus *Eucycloidea* Hudleston, 1888

Type species. *Turbo bianor* d'Orbigny, 1850. Upper Bajocian, Calvados (northern France).

Eucycloidea tenuistria (Münster in Goldfuss, 1841)

Figure 7l–s

1841 *Rostellaria tenuistria* Münster; Münster in Goldfuss, p. 16, pl. 169, fig. 9.

1841 *Rostellaria nodosa* Münster; Münster in Goldfuss, p. 16, pl. 169, fig. 10.

1844 *Trochus sedgwicki* Münster; Münster in Goldfuss, p. 53, pl. 179, fig. 4.

1844 *Turbo subangulatus* Münster; Münster in Goldfuss, p. 98, pl. 194, fig. 5.

1850 *Turbo patroclus* d'Orb.; d'Orbigny, p. 248.

1850 *Turbo Hero* d'Orb.; d'Orbigny, p. 266.

? 1853 *Turbo sedgwickii* Münster; d'Orbigny, p. 1853, p. 338, pl. 328, figs 9–11.

1853 *Purpurina patroclus* d'Orbigny; d'Orbigny, pl. 329, figs 9–11.

1858 *Turbo subangulatus* Quenstedt, p. 314, pl. 43, fig. 20.

1884 *Turbo subangulatus* Quenstedt, p. 429, pl. 202, figs 1–4.

1889 *Nortonia* (*Purpurina*) *patroclus* d'Orbigny; Wilson in Wilson & Crick, p. 299, pl. 9, figs 1a, b.

1901 *Amberleya tenuistria* Münster; Schlosser, p. 543.

1906 *Purpurina* (*Pseudalaria*) *patroclus* d'Orbigny; Cossmann, p. 209, pl. 8, fig. 10.

1908 *Turbo patroclus* d'Orbigny; Thevenin, p. 190, pl. 14, figs 3, 4.

1909 *Eucyclus subangulatus* (Münster); Brösamlen, p. 258, pl. 20, fig. 10.

1913 *Purpurina* (*Pseudalaria*) *patroclus* d'Orbigny; Cossmann, p. 171, pl. 8, figs 27–30.

1935 *Eucyclus subangulatus* (Münster); Kuhn, p. 137, pl. 10, fig. 4.

1966 *Amberleya* (*Eucyclus*) *tenuistria* (Münster); Klöcker, p. 239, fig. 8.

? 1997 "*Turbo*" sp.; Fischer & Weber, p. 134.

1997 *Eucycloidea* (*Pseudalaria*) *patroclus* (d'Orbigny); Fischer & Weber, p. 135, pl. 24, figs 3a, b.

2001 *Amberleya* (*Eucyclus*) *subimbricata* (d'Orbigny); Fürsich *et al*., p. 176, fig. 4D.

2001 *Eucycloidea* (*Pseudalaria*)? *subangulata* (Münster); Conti & Monari, p. 198, figs 15.26–28.

2009 *Eucyclus subangulatus* (Münster); Schulbert & Nützel, p. 478, fig. 3.

2013 *Eucycloidea tenuistria* (Münster); Schulbert & Nützel, p. 731, figs 8A–M.

Material. 7 specimens: MNHNL QH603, MNHNL QH604, MNHNL QH605 (2 specimens), UBGD 278820, UBGD 278821 (2 specimens), Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone. 2

specimens: MNHNL QH606, Cornus, Upper Toarcian, Aalensis Zone, Lugdunensis Subzone. 1 specimen: UBGD 278824, Tournadous, Lower Toarcian, Bifrons Zone, Bifrons Subzone. 8 specimens: MNHNL QH607 (3 specimens), UBGD 278822, UBGD 278823 (2 specimens), UBGD 278825, UBGD 278826, Tournadous, Lower Toarcian, Bifrons Zone. 2 specimens: UBGD 278827, UBGD 278828, Tournadous, transition Bifrons Zone to Variabilis Zone. 5 specimens: MNHNL QH608, MNHNL QH609, MNHNL QH610, UBGD 278829 (2 specimens), Tournadous, Upper Toarcian, condensed Thouarsense Zone to Dispansum Zone, Insigne Subzone. 4 specimens: UBGD 278830 (2 specimens), UBGD 278831 (2 specimens), Tournadous, Upper Toarcian, Dispansum Zone, Insigne Subzone. 2 specimens UBGD 278832, Tournadous, Upper Toarcian, Dispansum Zone. 5 specimens: UBGD 278833, Tournadous, Upper Toarcian, Dispansum Zone, Gruneri Subzone. 1 specimen: UBGD 278834, Tournadous, Upper Toarcian, Pseudoradiosa Zone.

Dimensions. See Table 1.

Description. Shell high-turbiniform to pagodiform, composed of 7-8 whorls. Height of last whorl about two thirds of shell height. Whorls distinctly angulated and keeled. Peripheral keel a rather swollen spiral cord dividing whorl surface into wide and sloping ramp and narrower, concave outer face. Ramp width almost twice width of outer face, slightly convex on early teleoconch whorls, then concave. Outer face subvertical or slightly inclined abapically towards axis and limited abapically by second, less definite, keeled angulation bordering abapical suture or covered by it. Base convex, somewhat swollen. Aperture semicircular and discontinuous on parietal lip. Inner lip thick, almost straight and extended in its lower part to form outlet at junction with basal lip. Early teleoconch whorls ornamented by moderately strong, prosocline and slightly opisthocyrt collabral ribs starting at adapical suture and fading below peripheral keel. Ribs producing slightly pointed nodes at adapical suture and on keel (about 30 on third whorl). Sutural ramp and outer face covered by 5-6 spiral threads each, forming rather regular network with collabral ribs. Subsutural spiral thread

slightly more robust but discontinuous. Small granules present at rib/thread intersections. Collabral ribs changing progressively into somewhat thin and sharp threads. Adult whorls bearing densely packed, very thin spiral threads, about 20 on ramp and about a dozen on outer face, separated by wider interspaces and running also over peripheral keel. Collabral threads forming small pointed nodes on keels and on subsutural spiral thread, and granules at intersections with other spiral threads. Nodes on peripheral keel larger than those on second angulation. Five very widely spaced, acute spiral cords on base between periphery and neck. Up to four more close-set and finer spiral cords on neck. Interspaces between cords showing same pattern of spiral and collabral threads as ramp and outer face. Growth lines prosocline and opisthocyrt on ramp, slightly prosocline to orthocline and gently prosocyrt on outer face, prosocyrt on base.

Remarks. Several authors (Schlosser, 1901; Brösamlen, 1909; Klöcker, 1966; Schulbert & Nützel, 2013) recognized the synonymy between *Rostellaria tenuistria* Münster, 1841, *Rostellaria nodosa* Münster, 1841, *Trochus sedgwicki* Münster, 1844 and *Turbo subangulatus* Münster, 1844 (see Klöcker, 1966 and Schulbert & Nützel, 2013 for further details). According to the dates of publication of the different parts of Goldfuss' monograph, the valid name of the species should be chosen between *R. tenuistria* and *R. nodosa*. In fact, both species were published in 1841 whereas *T. sedgwiki* and *T. subangulatus* were published three years later. The first reviser of the species was Schlosser (1901) who fixed the name *tenuistria* (ICZN 1999, Art. 24.2). As stated by Oppel (1856–1858), Giebel (1866) and Klöcker (1966), and suspected by Schlosser (1901), Brösamlen (1909) and Conti & Monari (2001), *Turbo patroclus* d'Orbigny, 1850 is another junior synonym of *E. tenuistria*. D'Orbigny (1853) ascribed to *T. sedgwicki* some specimens from the Toarcian of Alsace (eastern France). That material is lacking from d'Orbigny' collection and its species assignment cannot be verified (Fischer & Weber, 1997).

Distribution of the species. Undifferentiated Toarcian, Gard (southern France); Lower Toarcian, Leicestershire (central England); Lower to Upper Toarcian, Causses basin (southern France); Upper Toarcian, Cher (central France); undifferentiated Upper Toarcian–Lower Aalenian and Lower Aalenian, Franconia (southern Germany); Lower Aalenian, Swabia (southern Germany); Lower Bajocian, Central High Atlas (Morocco).

[Figure 8 here]

Superfamily NERITOPSOIDEA Gray, 1847

Family NERITOPSIDAE Gray, 1847

Genus *Neritopsis* Grateloup, 1832

Type species. *Neritopsis moniliformis* Grateloup, 1832. Lower Miocene, Aquitaine basin (western France).

Neritopsis philea d'Orbigny, 1850

Figure 8a–g

1850 *Neritopsis Philea* d'Orb.; d'Orbigny, p. 247.

1852 *Neritopsis Philea* d'Orb. d'Orbigny, p. 222, pl. 300, figs 5–7.

non 1874 *Neritopsis philea* (d'Orbigny); Dumortier, p. 133, pl. 34, figs 8–10.

1894 *Neritopsis philea* d'Orbigny; Hudleston, p. 341, pl. 27, figs 11a–c.

1909 *Neritopsis opalina* n.sp.; Brösamlen, p. 239, pl. 19, figs 21a, b.

1997 *Neritopsis philea* d'Orbigny; Fischer & Weber, p. 85.

2013 *Neritopsis opalina* Brösamlen; Schulbert & Nützel, p. 737, figs 11A–D.

Material. One specimen: UBGD 278835, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone.

Dimensions. See Table 1.

Description. Shell with low but distinctly elevated spire and rather globose last whorl. Teleoconch preserving last two rapidly expanding whorls separated by impressed sutures. Whorls strongly convex and rounded at periphery. Subsutural part of whorl flat and forming ramp orthogonal to spire axis and delimited by obtuse, moderately sharp shoulder. Base strongly convex and swollen. Narrow groove, probably a false umbilicus, present on axial region of base and encircled by shallow spiral bulge. Aperture seemingly semicircular and peristome discontinuous on parietal lip. Outer lip not preserved. Inner lip sharp and gently arched, detached from surface of base. Ornament mainly of spiral threads. Ramp of penultimate whorl ornamented by six, moderately strong spiral threads separated by somewhat narrow interspaces. Five to six, widely spaced spiral threads intercalated by secondary spiral thread on rest of whorl. Third order of spiral threads appearing in the interspaces between the primary and the secondary threads on last whorl. Shell fully covered by dense and strong growth lines making surface rough and spiral ornament waved. Occasional thin collabral threads forming a sort of network with spiral threads. Most prominent growth lines forming also small, sparsely distributed tubercles at intersection with spiral ornament, especially on outer edge of ramp. Growth lines prosocline, gently and widely prosocyrt on whorl surface and on base, opisthocyrt on axial region of base.

Remarks. *Neritopsis philea* d'Orbigny, 1851 is characterized by a flat subsutural ramp edged by an obtuse but sharp shoulder, a fully adult spiral ornament made of at least three orders of spiral threads progressively appearing during growth, and thin collabral threads or lines sparsely granulating the spiral threads. The same characters are present in *Neritopsis opalina* Brösamlen, 1909, a species originally instituted on a strongly fragmentary specimen and that is here considered as synonym of *N. philea*. This seems to be substantiated by the well preserved specimen recently

assigned by Schulbert & Nützel (2013) to *N. opalina* which clearly shows the characters listed above. Rollier (1918, p. 20) maintained that the material ascribed by Hudleston (1894) to *N. philea* belongs to a different species that he named *Neritopsis abbas* Rollier, 1918. Fischer & Weber (1997) supported his opinion. However, Hudleston's specimen does not seem to show differences sufficient to justify a species distinction. In agreement with Fischer & Weber (1997), the specimen coming from the Toarcian–Aalenian deposits of Isère (south-eastern France) ascribed by Dumortier (1874) to *N. philea* most likely does not belong to that species because it lacks a flat subsutural ramp. The same difference distinguishes *N. philea* from *Neritopsis spekei* (Moore, 1866) (p. 202, pl. 5, fig. 11), a species from the Toarcian deposits of Somerset (south-western England).

Distribution of the species. Undifferentiated Toarcian, Burgundy (southern France); Upper Toarcian, Causses basin (southern France); Lower Aalenian, Swabia and Franconia (southern Germany); Upper Aalenian, Dorset (south-western England).

Superfamily ZYGOPLEUROIDEA Wenz, 1938

Family ZYGOPLEURIDAE Wenz, 1938

Genus *Katosira* Koken, 1892

Type species. *Chemnitzia periniana* d'Orbigny, 1851. Pliensbachian, Saône-et-Loire (eastern France).

Katosira sp.

Figure 9a, b

Material. One specimen: MNHNL QH611, Tournadous, Lower Toarcian, Bifrons Zone.

Dimensions. See Table 1.

Description. Shell high-spired, slightly cyrtoconoid, preserving last seven whorls. Whorls almost twice as wide as high, regularly convex, the convexity tending to attenuate slightly during growth. Suture distinctly inclined. Base anomphalous, slightly convex and seemingly encircled by rounded angulation. Aperture elliptical-ovate, angulated at sutural corner and apparently lacking siphonal outlet. Inner lip thin, gently arched and slightly detached from surface of base. Sparse shell remains with traces of about a dozen collabral ribs per whorl, roughly aligned to each other between adjacent whorls. Collabral ribs sharp, evenly spaced, slightly opisthocline and parasigmoidal, distinctly opisthocyrt on most of whorl surface and prosocyrt in its abapical band. Weak and narrow subsutural bulge (spiral thread?) on inner mould.

Remarks. The specimen is represented by an inner mould with sparse remains of the shell wall that does not consent a safe species attribution. It strongly resembles *Scalaria liasica* Quenstedt, 1852 (p. 418, pl. 33, fig. 27; Oppel, 1854, p. 98, pl. 3, figs 13, ?14; Quenstedt, 1856, p. 152, pl. 19, figs 5–12, 1884, p. 307, pl. 196, figs 66, 67, 69–73, ?68) from the Pliensbachian of Swabia and Franconia (southern Germany). Other similar species are *Katosira carusensis* (d'Orbigny, 1850) (p. 226; d'Orbigny, 1851, p. 34, pl. 237, figs 13–15; Fischer & Weber, 1997, p. 13, pl. 1, fig. 10) from the Lower Pliensbachian of Cher (central France) and *Katosira corvaliana* (d'Orbigny, 1851) (p. 37, pl. 343, fig. 4; Fischer & Weber, 1997, p. 15, pl. 1, figs 6a, b) from the Pliensbachian of Saône-et-Loire (eastern France). However, Fischer & Weber (1997) defined the collabral ribs of *K. corvaliana* as "orthocyrtes" whereas in the specimen here described they are parasigmoidal. *Katosira*? sp. described by Gründel (2011*a*, p. 87, pl. 1, figs 5, 6), from the latest Pliensbachian of the Franconian Jura differs in being bigger and in having a lower number of collabral ribs which are also more opisthocline.

Distribution of the species: Lower Toarcian, Causses basin (southern France).

Superfamily CERITHIOIDEA Fleming, 1823

Family PROCERITHIIDAE Cossmann, 1905

Genus *Procerithium* Cossmann, 1902

Type species. *Procerithium quinquegranosum* Cossmann, 1902. Hettangian, Vendée (western France).

Procerithium pseudocostellatum (d'Orbigny, 1850)

Figure 9c–s

? 1842*b Melania undulata* Var. b E.-D.; Eudes-Deslongchamps, p. 217, pl. 11, figs 59, 60, non figs 61, 62.

1844 *Cerithium costellatum* Münster; Münster in Goldfuss, p. 31, pl. 173, fig. 8.

1850 *Cerithium pseudocostellatum* d'Orb.; d'Orbigny, p. 250.

? 1850 *Cerithium Jole* d'Orb.; d'Orbigny, p. 250.

1874 *Chemnitzia ferrea* nov. sp.; Dumortier, p. 129, pl. 35, fig. 8.

1884 *Cerithium costellatum* Goldfuss; Quenstedt, p. 516, pl. 205, figs 40, 41.

? 1908 *Cerithium Jole* d'Orb.; Thevenin, p. 191, pl. 14, figs 7, 8.

1913 *Procerithium* (*Rhabdocolpus*) *pseudocostellatum* d'Orbigny; Cossmann, p. 71, pl. 3, figs 106–108.

? 1913 *Procerithium* (*Rhabdocolpus*) *jole* d'Orbigny; Cossmann, p. 71, pl. 4, figs 1, 18, 19.

1923 *Cryptaulax subarmata* sp. n.; Ernst, p. 70, pl. 1, figs 20a, b.

? 1999*a Procerithium compactum* n.sp.; Gründel, p. 4, pl. 1, figs 7–9.

? 2009 *Procerithium compactum* Gründel; Schulbert & Nützel, p. 489, fig. 10.

? 2013 *Procerithium compactum* Gründel; Schulbert & Nützel, p. 742, figs 14H–J.

Material. Six specimens: MNHNL QH612, MNHNL QH613, UBGD 278836, UBGD 278837, UBGD 278838, UBGD 278839, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone.

Dimensions. See Table 1.

Description. Shell turritelliform, slightly gradate and composed of about ten whorls. Apical shell seemingly slightly coeloconoid, adult shell weakly cyrtoconoid. Whorls twice as wide as high. Height of last whorl slightly more than one third of shell height. Whorls flat to very slightly convex, with narrow, scarcely defined ramp. Suture almost grooved. Base low-conical and slightly convex. Aperture not completely preserved. Inner lip seemingly slightly detached from surface of base. Ornament made by collabral ribs and spiral threads. Collabral ribs rather strong, weakly opisthocline, straight to gently opisthocyrt, about twelve per whorls on fully adult shell, separated by wider interspaces and roughly aligned to each other between adjacent whorls. Four to five, equally spaced, quite marked spiral threads forming little nodes at intersection with collabral ribs. Subsutural spiral thread edging ramp and slightly more marked. Five to six, evenly spaced and equally sized spiral threads visible on base. Growth lines slightly opisthocline and opisthocyrt on whorl surface, not observable on base.

Remarks. D'Orbigny (1850) changed in *pseudocostellatum* the name *Cerithium costellatum* Münster in Goldfuss, 1844 to avoid secondary homonymy with *Nassa costellata* Sowerby in Fitton, 1836, a species from the Albian of Blackdown Hills (south-western England) that he considered as belonging to *Cerithium*. The type material of *C. costellatum* comes from the Lower Jurassic of Pretzfeld (Franconia). The main teleoconch characters of *Procerithium pseudocostellatum* (d'Orbigny, 1850) are also present in *Procerithium compactum* Gründel, 1999, a species from the

Upper Toarcian to Lower Aalenian of Franconia (southern Germany). Gründel's species could be a synonym of *P. pseudocostellatum* but the lack of information on the protoconch of the latter species does not permit to assess with certainty the relationship between the two taxa.

Cryptaulax subarmata Ernst, 1923, which Gründel (1999*a*) tentatively included in the synonymy list of *Cryptaulax armata* (Goldfuss, 1843) does not seem to show differences sufficient to keep it distinct from *P. pseudocostellatum*. In contrast, as rightly established by Gründel (1999*a*), the material figured by Kuhn (1935, p. 144, pl. 8, figs 6a, b) as *C. subarmata* belongs to *Procerithium brandi* (Walther, 1951). That species differs from *P. pseudocostellatum* in having lower and more convex whorls, a slightly wider and sloping subsutural ramp, and more numerous axial ribs per whorl (18–20) in the adult shell.

Procerithium jole (d'Orbigny, 1850) is another possible synonym of *P. pseudocostellatum*. Cossmann (1913) assigned to this species also the specimen figured by Eudes-Deslongchamps (1842*b*) in pl. 11, fig. 59 as var. b of *Melania undulata* Eudes-Deslongchamps, 1842. According to Cossmann (1913), *P. jole* differs from *P. pseudocostellatum* in having a smaller size, a less spiny subsutural spiral thread, and an additional spiral thread on the whorl surface. Based on the analysis of the material studied here and of the past literature, these differences could be accommodated within the morphological variability of *P. pseudocostellatum.*

Distribution of the species. Undifferentiated Toarcian, Franconia (southern Germany), Aude (southern France), Mont d'Or (central southern France), Alsace and Doubs (eastern France); Upper Toarcian, Lower Saxony (northern Germany) and Causses basin (southern France); Lower Aalenian, Alsace (eastern France).

[Figure 9 here]

Genus *Cryptaulax* Tate, 1869

Type species. *Procerithium* (*Xystrella*) *protortile* Cox, 1969, nom. nov. pro *Cerithium tortile* Hébert & Eudes-Deslongchamps, 1860 non Eudes-Deslongchamps, 1842. Lower Callovian, Maine-et-Loire (western France).

Cryptaulax armata (Goldfuss, 1843)

Figure 9t–v

1831 *Turritella echinata* Buch, pl. 7, fig. 1.

1836 *Turritella echinata* Buch; Bronn, p. 395, pl. 21, fig. 24.

1843 *Cerithium armatum* nobis; Goldfuss, p. 31, pl. 173, fig. 7.

1858 *Cerithium armatum* Goldfuss; Quenstedt, p. 315, pl. 43, fig. 22.

1884 *Cerithium armatum* Goldfuss; Quenstedt, p. 515, pl. 205, figs 37–39.

1887 *Cerithium armatum* Goldfuss; Denckmann, p. 83, pl. 9, figs 6, 6a.

1906 *Cerithium* (*Xystrella*) *armatum* Münster; Cossmann, p. 30, pl. 5, fig. 26.

1909 *Cryptaulax armata* Goldfuss; Brösamlen, p. 291, pl. 21, figs 27–29.

1913 *Procerithium* (*Xystrella*) *armatum* (Goldfuss); Cossmann, p. 85, pl. 4, figs 45–49, 51–53.

1935 *Cryptaulax armata* Goldfuss; Kuhn, p. 144,, pl. 8, figs 25a, b, pl. 9, fig. 4, pl. 10, fig. 36.

? 1937 *Cryptaulax armata* Goldfuss; Pčelincev, p. 37, pl. 5, fig. 9.

? 1937 *Cryptaulax armata* var. *ornata* Pčelincev; Pčelincev, p. 38, 68, pl. 2, fig. 61.

1951 *Procerithium* (*Xystrella*) *echinatum* (von Buch); Walther, p. 79, pl. 4, figs 7a, b.

1997 *Procerithium armatum* (Goldfuss); Gründel, p. 96, pl. 6, figs 6–9.

1999*a* *Cryptaulax armatum* (Goldfuss); Gründel, p. 19, pl. 5, figs 1–4.

2001 *Cryptaulax* (*Xystrella*) *armata* (Goldfuss); Fürsich *et al*., fig. 4L.

2004 *Cryptaulax armata* (Goldfuss); Kaim, p. 37, fig. 22.

2009 *Cryptaulax armatum* (Goldfuss); Schulbert & Nützel, 488, figs 9A–D.

2013 *Cryptaulax armatum* (Goldfuss); Schulbert & Nützel, 740, figs 13A–D.

Material. Five specimens: MNHNL QH614, MNHNL QH615, MNHNL QH616 (three specimens), Tournadous, Lower Toarcian, Bifrons Zone, Bifrons Subzone.

Dimensions. See Table 1.

Description. Shell small, high-spired and slender. Spire composed of about a dozen whorls. Whorls about twice as wide as high. Height of last whorl less than one third of shell height. Whorls almost flat and limited by flush sutures. Base somewhat low, evenly convex and anomphalous. Ornament composed of three spiral threads persisting up to the last whorl. Upper and lower threads bearing prominent nodes and running near adapical and abapical suture, respectively. Lower thread marking periphery of whorl. Median thread closer to the upper thread and with smaller nodes. Nodes formed by intersection of spiral threads with slightly prosocline collabral ribs. Fourth thinner spiral thread sometimes between median and abapical threads. Fully adult whorls sculptured by nine to ten collabral ribs roughly aligned between adjacent whorls. Abaxial half of base ornamented by two spiral threads having nodes as prominent as those of median thread. Most abaxial thread of base covered by suture. Adaxial region of base not preserved.

Remarks. *Cerithium armatum* was apparently introduced by Goldfuss (1843) as a replacement name for *Turritella echinata* Buch, 1831. This last had been included in *Cerithium* by several authors (Roemer, 1836, p. 141, 1839, p. 3; Koch & Dunker,1837, p. 10; Buch, 1839, p. 104), thus becoming a secondary homonym of the Recent *Cerithium echinatum* Lamarck, 1822. Subsequently, there has been considerable confusion about the nomenclatural status of these taxa. Quenstedt (1852, 1858, 1884), for example, treated *C. armatum* and *C. echinatum* as distinct species. In his opinion the two taxa are extremely similar but could be differentiated based on stratigraphical distribution, i.e. Braunen Jura α for *armatum* and Braunen Jura ε for *echinatum*. Brösamlen (1909) and, more

recently, Kaim (2004) also kept separate the two species even if they report specimens with transitional morphologies. According to the first author (Brösamlen 1909, p. 292), *Cryptaulax echinata* could be distinguished by the slenderer shape, the higher whorls, the higher number of collabral ribs and the narrower sutural groove. Walther (1951) stated that the material referred to Buch's *echinata* by Quenstedt (1858, 1884), and Brösamlen (1909) is to be ascribed to a new taxon, *Procerithium* (*Xystrella*) *quenstedti* Walther, 1951. He included *armatum* in the synonymy of *Procerithium* (*Xystrella*) *echinatum* arguing that Goldfuss' name is invalid being a younger synonym. As a matter of fact, *Turritella echinata* Buch, 1831 and *Cerithium armatum* Goldfuss, 1843 are objective synonyms (ICZN 1999, Art. 72.7) and Buch's name is permanently invalid, though no longer considered congeneric with Lamarck's taxon, because it was replaced before 1961 (ICZN 1999, Art. 59.3).

A rather wide morphological variability of teleoconch ornaments, especially concerning the number, persistence and thickness of secondary spiral threads, has been described in *C. armata* (see descriptions in Brösamlen, 1909; Cossmann, 1913; Gründel, 1999*a*; Kaim, 2004). The median spiral thread can attain the same strength of the two main nodular spiral threads, but it can also disappear during the growth or be totally lacking. The number of collabral ribs is also variable. In the specimens here described, the median spiral thread is slightly less robust than the main ones and persists until the last whorl. A fourth intercalary thread is sometimes developed. The specimens are very similar to those figured by Cossmann (1913, pl. 4, figs 45, 46 and 51) from the Toarcian of Metz (Lorraine, eastern France) and by Schulbert & Nützel (2013, fig. 13) from the Upper Toarcian–Lower Aalenian of Mistelgau (Franconia, southern Germany).

It is very difficult to differentiate *Cryptaulax quenstedti* (Walther) (= *C. echinata* sensu Quenstedt and Brösamlen) from *C. armata*, especially taking into account the morphological variability reported for both species. Walther's taxon could well be a synonym of *C. armata*. *Cryptaulax scobina* (Eudes-Deslongchamps, 1842*a*) (p. 196, pl. 10, figs 49, 50) from the Upper

Pliensbachian of Calvados (northern France) has the same ornamentation pattern of *C. armata*, but its shell is more slender and has a subcylindrical shape.

Distribution of the species. Undifferentiated Toarcian, Lorraine (eastern France) and Calvados (northern France); Undifferentiated Toarcian and Lower Aalenian, Alsace (eastern France); Lower Toarcian, Causses basin (southern France); Upper Toarcian, Lower Saxony (northern Germany); Upper Toarcian to Lower Aalenian, Franconia (southern Germany); Lower Aalenian, Swabia (southern Germany); Middle Bathonian, Częstochowa region (south-western Poland).

Superfamily AMPULLINOIDEA Cossmann, 1919

Family AMPULLINIDAE Cossmann, 1919

Genus *Ampullospira* Harris, 1897

Type species. *Euspira canaliculata* Morris & Lycett, 1851. Aalenian–Bajocian, Yorkshire (north-eastern England).

Ampullospira pelops (d'Orbigny, 1850)

Figure 9w–z

1850 *Natica Pelops* d'Orb., d'Orbigny, p. 247.

1852 *Natica Pelops* d'Orb.; d'Orbigny, p. 188, pl. 288, figs 16, 17.

1874 *Natica Pelops* (d'Orbigny); Dumortier, p. 131, pl. 34, figs ?5, 6, 7.

1884 *Natica pelops* d'Orbigny; Quenstedt, p. 273, pl. 194, fig. 59.

1909 *Natica pelops* d'Orbigny; Brösamlen, p. 266, pl. 20, fig. 29.

1925 *Ampullospira pelops* (d'Orb.); Cossmann, p. 49, pl. 5, figs 1, 2.

non 1937 *Natica pelops* d'Orb.; Pčelincev, p. 33, pl. 2, figs 39, 40.

1997 *Ampullospira pelops* (d'Orbigny); Fischer & Weber, p. 69, pl. 17, fig. 5.

? 2002 *Ampullospira* (*Ampullospira*) cf. *pelops* (d'Orbigny); Gahr, p. 130, pl. 5, fig. 16.

Material. Two specimens: UBGD 278840, Tournadous, Lower Toarcian, Bifrons Zone, Bifrons Subzone. One specimen: UBGD 278841, Tournadous, upper Lower to Upper Toarcian, exact stratigraphical level unknown.

Dimensions. See Table 1.

Description. Shell rather globose, composed of very convex whorls separated by strongly impressed sutures. Last whorl swollen, its height almost 90% of shell height. Upper band of whorl surface forming a slightly convex ramp almost orthogonal to spire axis. Ramp outer edge rounded on first observable whorls, becoming progressively more distinct on final half of last whorl. Base globose, high and downward elongated. Aperture ovate, wider in its upper half.

Remarks. The material consists of inner moulds preserving some remains of a thin shell wall. The outline of the shell and the rate of growth of the spire correspond to those of *Ampullospira pelops* (d'Orbigny, 1850). However, the specimens are distinctly smaller and are probably represented by not fully adult shells. The material ascribed by Hudleston 1892 (p. 259, pl. 20, figs 2–6) to *Natica adducta* Phillips, 1829 from the Aalenian–Bajocian of England differs in having a flatter ramp bordered by a sharper outer rim.

The specimen from the Toarcian deposits of Caucasus ascribed by Pčelincev (1937) to *Natica pelops* differs from the type material and from the specimens here described in having a more elongated shell, less swollen whorls, and a more oblique and less distinct ramp.

Distribution of the species. Undifferentiated Toarcian, Sarthe (north-western France), Isère (south-eastern France); Lower and ?Upper Toarcian, Causses basin (southern France); Upper Toarcian, Swabia (southern Germany).

4. Considerations on the recovery after the Early Toarcian anoxic event

The systematic analysis allowed the recognition of 15 species, two of which in open nomenclature. Two species, namely *Angulomphalus expansus*, *Pleurotomaria amalthei* and the material here dubitatively referred to *Ooliticia*? *cyclostoma*, come from Upper Pliensbachian beds (Margaritatus Zone, Gibbosus Subzone) of the Marnes de Villeneuve Fm. All these species are typical of the western European gastropod communities of that age. The other species were collected from the Toarcian part of the Marnes de Fontaneilles Fm. (Fig. 10). Fürsich *et al*. (2001, tab.1), in their palaeoenvironmental analysis of some Toarcian sections of the Causses basin, recognized six gastropod species, namely *Pleurotomaria* sp., *Amberleya subimbricata* (=*Eucycloidea tenuistria*), *Eucyclus capitaneus*, *Costatrochus subduplicatus*, *Procerithium* sp. and *Cryptaulax armata*. Except for *E. capitaneus*, the taxa determined at species level have been found also in the sections of Tournadous and Cornus. In agreement with Fürsich *et al*. (2001), most probably the gastropods represented epifaunal mobile, soft bottom dwellers belonging to macrobenthic associations with low to moderate species diversity.

[Figure 10 here]

The gastropod fauna here described adds further details to the reconstruction of the faunal recovery history after the Early Toarcian anoxic event depicted by Fürsich *et al*. (2001) for the Causses basin. The stratigraphical distribution of the species shows two peaks of relative diversity, i.e. in the Bifrons Zone, mainly Bifrons Subzone, and in the Aalensis Zone, Mactra Subzone (Fig. 10). Nine species occur in the Bifrons Zone. Five of them, namely *Bathrotomaria kronzwilmesorum*, *C. subduplicatus*, *E. tenuistria*, *Cryptaulax armata* and *Ampullospira pelops*,

were collected in the Bifrons Subzone. The part of Tournadous section yielding the other four species (*Sisenna canalis*, *Eucyclus escheri*, *Eucyclus elegans* and *Katosira* sp.) cannot be safely ascribed to a distinct subzone, although it is strongly suspected to represent the Bifrons Subzone. *S. canalis*, *E. escheri* and *E. elegans*, are recorded in Pliensbachian localities of NW Europe and can be interpreted as survivors from the pre-event stock (Fig. 10).The first known occurrence of the remaining species is subsequent to the anoxic event. In the beds including the Variabilis to Pseudoradiosa Zones, gastropods are represented only by *C. subduplicatus* and *E. tenuistria* or are absent. The peak of diversification in the Aalensis Zone is much less pronounced, being represented by five species only (*Pleurotomaria escheri*, *C. subduplicatus*, *E. tenuistria*, *Neritopsis philea* and *Procerithium pseudocostellatum*). The component inherited from the pre-event faunas is limited to a single species, namely *P. escheri*. This peak falls entirely into the Mactra Subzone whereas in the Fluitans Subzone, again, only *C. subduplicatus* and *E. tenuistria* occur. Except from these latter, the species of the Aalensis stock are different from those of the Bifrons stock.

According to Fürsich *et al*. (2001), the changes in the macrobenthic associations recorded in the Causses succession after the Early Toarcian anoxic event are related to changes in oxygenation and substrate consistency. In the lower part of the sequence, the low diversity reflects oxygen fluctuations, whereas the extremely soupy substrate resulting from the activity of burrowing organisms was the main controlling factor in the Late Toarcian time. In this scenario, the peaks of the Bifrons and Aalensis Zones documented in the present study would reflect brief times during which the oxygen content and bottom consistency favoured the settlement of a relatively diversified fauna. The exclusive occurrence of *C. subduplicatus* and *E. tenuistria* in the interval between the Variabilis and Pseudoradiosa Zones could indicate more severe and unstable environmental conditions allowing survival only to gastropod taxa with wide adaptive capacities. As a matter of fact, these two species show the typical features of the opportunistic taxa, e.g. wide morphological variability, long stratigraphical range, absolute dominance in low-diversity associations and

accessory occurrence in diversified associations. Presumably, this low-diversity depended mostly on the diffusion of soupy substrates, as indicated by Fürsich *et al*. (2001).

Additional information can be deduced from the comparison of the gastropod fauna of the Causses basin with the Upper Toarcian–Lower Aalenian fauna of Mistelgau (Franconia, southern Germany) recently analysed by Schulbert & Nützel (2009, 2013) with a comparable stratigraphical detail. The two faunas show substantial differences. In the Causses basin the species diversity is much lower than at Mistelgau. This might be in part due to different sampling methods (bulk samples and surface collection in the case of Mistelgau), though the low diversity of gastropods in the Causses basin is confirmed by the analysis based on quantitative sampling provided by Fürsich *et al*. (2001). Schulbert & Nützel (2013) described 26 species in the Upper Toarcian sediments, mainly Caenogastropoda and Heterobranchia, and the most represented taxa are *Coelodiscus minutus* and *Toarctocera subpunctata*. Those authors observed that, in general, the degree of diversity is comparable with that of the faunas preceding the anoxic event. In the Causses basin the Vetigastropoda clearly prevail and the Heterobranchia are absent. *C. minutus* and *T. subpunctata* are lacking whereas the most abundant species are *C. subduplicatus* and *E. tenuistria*. Both these species occur from the Bifrons Zone and persist throughout the sections up to the end of the Toarcian. At Mistelgau, *E. tenuistria* is recorded only in the Lower Aalenian sediments. The dominance of *C. subduplicatus* and *E. tenuistria* has been recognized also by Fürsich *et al*. (2001, fig. 18) in other sections of the Causses basin. Thus, it seems to be a characteristic aspect of the Toarcian gastropod faunas of this basin. These differences do not seem to be related to significant facies differences. Both the Mistelgau and Causses successions consist mostly of homogenous clays and marls deposited in quiet environments with diffused soupy substrates, below storm wave base and in fully aerobic to dysaerobic conditions (Fürsich *et al*. 2001; Schulbert & Nützel, 2013).

[Figure 11 here]

The trend of faunal recovery after the Early Toarcian crisis also differs in the two areas. Schulbert & Nützel (2013, fig. 3) showed a progressive increase of species diversity from the

Levesquei Zone to the Aalensis and Opalinum Zones. According to those authors, this diversity gradient was probably driven by a progressive rise of oxygen concentration and represents the recovery and turnover of gastropod communities after the anoxic event in Franconia. In contrast, this process was much slower and discontinuous in the Causses basin. These contrasting recovery patterns could be better understood by considering local physiographic factors and the position of the two basins in a wider palaeogeographic setting (Fig. 11). In the Toarcian, the Mistelgau area was part of a wide epicontinental seaway west of the Bohemian Massif (Schulbert & Nützel, 2013) having open communications and easy faunal exchanges with the other western European basins (Thierry, 2000). Conversely, the Causses region was a small intracratonic basin at the southern margin of the European shallow-water shelf, tightly confined by exposed lands of the Montagne Noire and the Massif Central and with Cévennes High hampering eastward communications (Baudrimont & Dubois, 1977; Trümpy, 1983; Mailliot *et al*. 2009). The southern side of the basin was open towards the central part of western Tethys (Trümpy, 1983), as also suggested by the relative mixing of NW Europe and Mediterranean pelagic faunas inhabiting the Causses basin after the Early Toarcian crisis (Guex, 1972, Pinard *et al*. 2014). However, repopulation of the benthic communities seems not to have benefited from the same Tethyan influx. Gastropod species of the Causses basin are very characteristic and exclusive components of the Toarcian–Early Aalenian communities of the European epicontinental seas and species from the central region of western Tethys are absent (Fig. 11). The Toarcian successions of central western Tethys are represented by pelagic sediments, such as red marly clays, nodular marls and condensed limestones, and by deposits of marginal and intra-oceanic carbonate platforms (Bernoulli & Jenkyns, 1974; Winterer & Bosellini, 1981; Farinacci & Elmi, 1981; Dercourt *et al*. 2000; Marino & Santantonio, 2010 and references therein). They reflect environmental conditions very different from those of the Causses basin where the Toarcian facies are instead roughly comparable to those of other regions of the western European shelf. Speculating from these evidences, gastropods of the central western Tethys that in theory could have reached easily the Causses region by dispersal, were probably unable to

settle and colonize that area due to the very different environment. On the other hand, the relative geographic isolation and marginal location of the Causses basin probably made the faunal exchange with the western European epicontinental seas difficult, determining the slow and discontinuous faunal recovery observed. Useful insights to test this interpretation might derive from the study of the mode of recovery of other benthic groups and by extending the analysis to the Aalenian faunas.

Acknowledgements. We thank Guy Kronz, Robert Haas, Andrea Di Cencio, Alain Faber (Palaeontological Department, National Museum of Natural History, Luxembourg) and Nino Mariotti (Department of Earth Sciences, University La Sapienza, Rome, Italy) who contributed to the field work. A. Nützel (Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany) and an anonymous reviewer provided valuable comments on the manuscript. The photographic work was executed by Stefano Castelli, and the preparation of the material was carried out by Lorenzo Franceschin (both Department of Geosciences, University of Padua, Italy). This paper was supported by the fund of the University of Padua (RG, SM grant number CPDA131234), by the Fonds National de la Recherche, Luxembourg (J-DP) and is a contribution to the INTERVIE (INSU) research program and to the BioME team of the Biogéosciences laboratory, Dijon, France (PN).

Declaration of Interest. None.

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FIGURE CAPTIONS

Figure 1. (a) Locality map of the studied area. (b) Palaeogeographic setting of the Causses basin at the Toarcian stage (simplified from Morard, unpub. Ph.D. Thesis, Université de Lausanne, 2004); white stars indicate studied sections.

Figure 2. Stratigraphical columns of the Late Pliensbachian-Toarcian succession cropping out at Tournadous and Cornus. Gastropod symbols: beds yielding gastropods. Question marks (?) indicate absence of stratigraphical markers. Standard zonation scheme from Page (2003).

Figure 3. Measurements of the specimens reported in the systematic descriptions and in Table 1. Abbreviations for the dimensions are as follows: H, height of the shell; HL, height of the last whorl; HA, height of the peristome; W, width of the shell; WA, width of the peristome; α, mean spire angle.

Figure 4. Eotomarioidea and Ptychomphaloidea. (a–l) *Sisenna canalis* (Münster in Goldfuss, 1844): (a–c) dorsal, basal and apertural views, MNHNL QH580; (d–f) apical and dorsal views, and detail showing the pattern of growth lines, MNHNL QH577; (g–h) apertural and dorsal views, MNHNL QH578; (i–l) dorsal, basal, apertural and apical views, MNHNL QH579. Tournadous, Lower Toarcian, Bifrons Zone. (m–r) *Angulomphalus expansus* (Sowerby, 1821): apertural, lateral and dorsal views, detail of the selenizone of the penultimate whorl, apical view, and detail of the whorl surface, MNHNL QH619, Tournadous, Upper Pliensbachian, Margaritatus Zone, Gibbosus Subzone; st: suture; sz: selenizone.

Figure 5. Pleurotomarioidea. (a–d) *Pleurotomaria amalthei* Quenstedt, 1858: dorsal, apical and apertural views, and detail of the whorl surface, UBGD 278805, Tournadous, Upper Pliensbachian, Margaritatus Zone, Gibbosus Subzone. (e–h) *Pleurotomaria escheri* Goldfuss, 1844: dorsal, apical and subapertural views, and detail of the whorl surface, MNHNL QH581, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone. (i–q) *Bathrotomaria kronzwilmesorum* sp. nov.: subapertural and apical view, detail of the early spire, dorsal, basal and lateral views, details of the fourth whorl, apex and last whorl, holotype MNHNL QH620, Tournadous, Lower Toarcian, Bifrons Zone, Bifrons Subzone.

Figure 6. (a–w) *Costatrochus subduplicatus* (d'Orbigny, 1850): (a–b) dorsal and apertural views, MNHNL QH617; (c–e) dorsal, apertural and basal views, MNHNL QH618. Tournadous, Lower Toarcian, Bifrons Zone; (f–h) basal, dorsal and apertural views, MNHNL QH595; (i–k) basal, dorsal and subapertural views, MNHNL QH597, Tournadous, Upper Toarcian, Aalensis Zone, Mactra Subzone; (l–n) basal, dorsal and apertural views, MNHNL QH582; (o–q) apertural, basal and dorsal views, MNHNL QH584; (r–t) apertural, basal and dorsal views, MNHNL QH585; (u–w) sublateral, basal and dorsal views, MNHNL QH583, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone.

Figure 7. Eucycloidea. (a–e) *Eucyclus escheri* (Münster in Goldfuss, 1844): (a–c) dorsal, apertural and basal views, MNHNL QH599; (d–e) dorsal and apertural views, MNHNL QH600, Tournadous, Lower Toarcian, Bifrons Zone. (f–h) *Eucyclus elegans* (Münster in Goldfuss, 1844): dorsal, basal and apertural views, MNHNL QH601, Tournadous, Lower Toarcian, Bifrons Zone. (i–k) *Ooliticia*? *cyclostoma* (Benz in Zieten, 1832) apertural, basal and dorsal views, UBGD 278819, Tournadous, Upper Pliensbachian, Margaritatus Zone, Gibbosus Subzone. (l–s) *Eucycloidea tenuistria* (Münster in Goldfuss, 1844): (l–n) basal, dorsal and apertural views, MNHNL QH603; (o–p) dorsal and

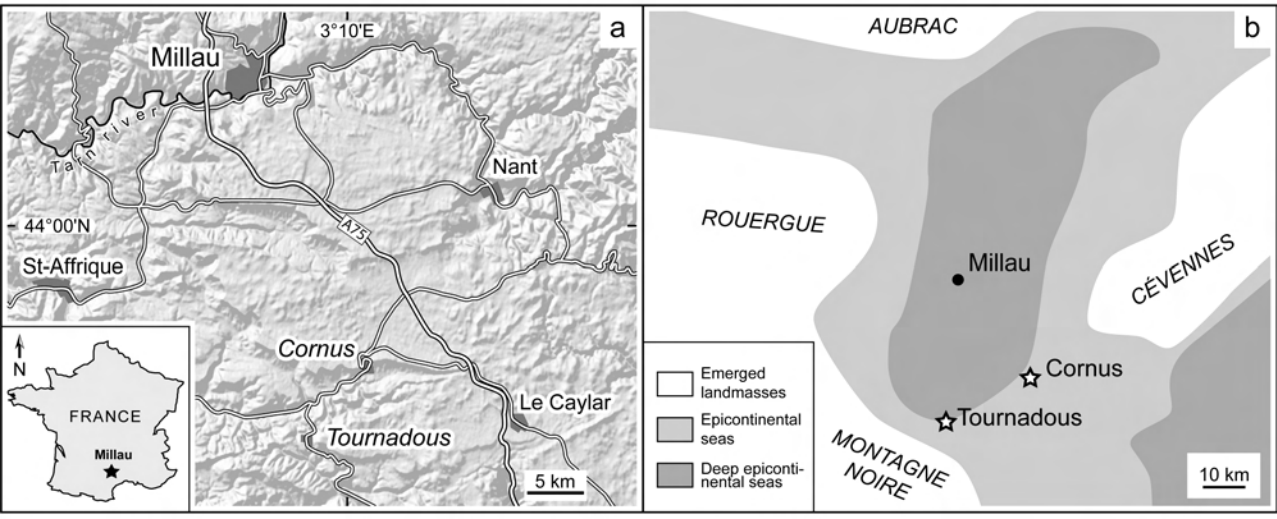
subapertural views, MNHNL QH604; (q–s) basal, apertural and dorsal views, UBGD 278820, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone.

Figure 8. (a–g) *Neritopsis philea* d'Orbigny, 1851: lateral, basal, apical, lateral (opposite), apertural views, detail of the ornament, and dorsal view, UBGD 278835, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone.

Figure 9. Zygopleuroidea, Cerithioidea and Ampullinoidea. (a–b) *Katosira* sp. apertural and dorsal views, MNHNL QH611, Tournadous, Lower Toarcian, Bifrons Zone. (c–s) *Procerithium pseudocostellatum* (d'Orbigny, 1850): (c–e) apertural, lateral and basal views, UBGD 278836; (f–h) basal, dorsal and apertural views, MNHNL QH612; (i–k) dorsal, apertural and lateral views, UBGD 278838; (l–o) detail of the ornament, dorsal, apertural and lateral views, UBGD 278837; (p–s) lateral, apertural, dorsal and basal views, UBGD 278839, Cornus, Upper Toarcian, Aalensis Zone, Mactra Subzone. (t–v) *Cryptaulax armata* (Goldfuss, 1843): (t–u) lateral and dorsal views, MNHNL QH614; (v) detail of the ornament, MNHNL QH615, Tournadous, Lower Toarcian, Bifrons Zone, Bifrons Subzone. (w–z) *Ampullospira pelops* (d'Orbigny, 1850): apical, apertural, basal and dorsal views, UBGD 278841, Tournadous, upper Lower to Upper Toarcian, exact stratigraphical level unknown.

Figure 10. Stratigraphical distribution of the species studied in the Causses basin and comparison with their overall stratigraphical distribution in other localities of the western European epicontinental shelf (see text for details).

Figure 11. Toarcian-Early Aalenian palaeogeographic distribution of the species described. Map and depositional environments based on Dercourt et al. (2000). Asterisk indicates the studied area.


a
Millau
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St-Affrique
Cornus
Le Caylar
Tournadous
5 km
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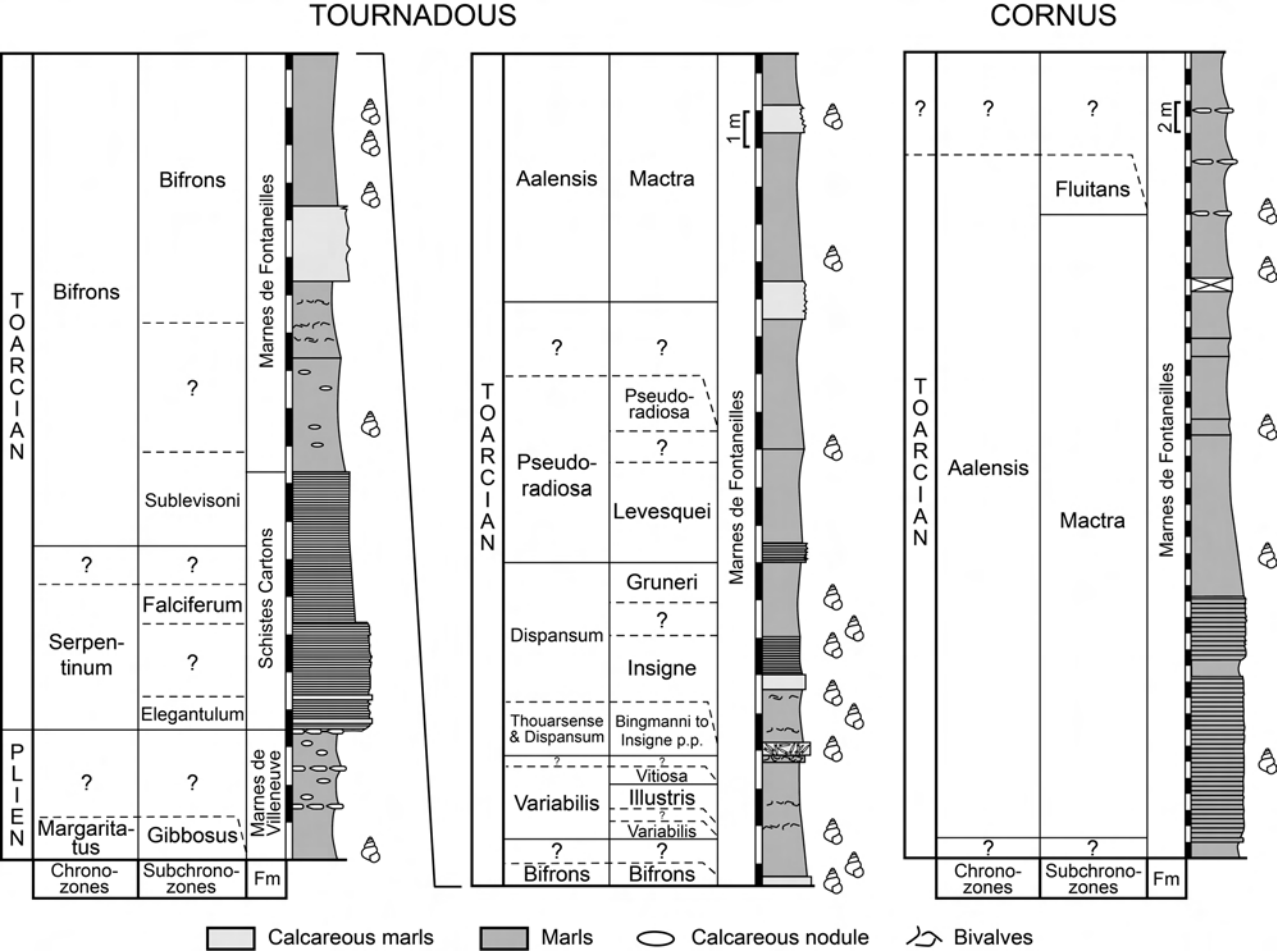
FRANCE
Millau
b
AUBRAC
ROUERGUE
Millau
CÉVENNES
Cornus
Tournadous
MONTAGNE NOIRE
Emerged landmasses
Epicontinental seas
Deep epicontinental seas
10 km


TOURNADOUS
CORNUS
TOARCIAN
PLIENSBACHIAN
Bifrons
?
Sublevisoni
?
Falciferum
?
Elegantulum
?
Gibbosus
Margaritatus
Serpentinum
Marnes de Fontanelles
Schistes Cartons
Marnes de Villeneuve
Aalensis
Mactra
Pseudo-radiosa
Levesquei
Gruneri
Insigne
Dispansum
Thouarsense & Dispansum
Bingmanni to Insigne p.p.
Vitiosa
Illustris
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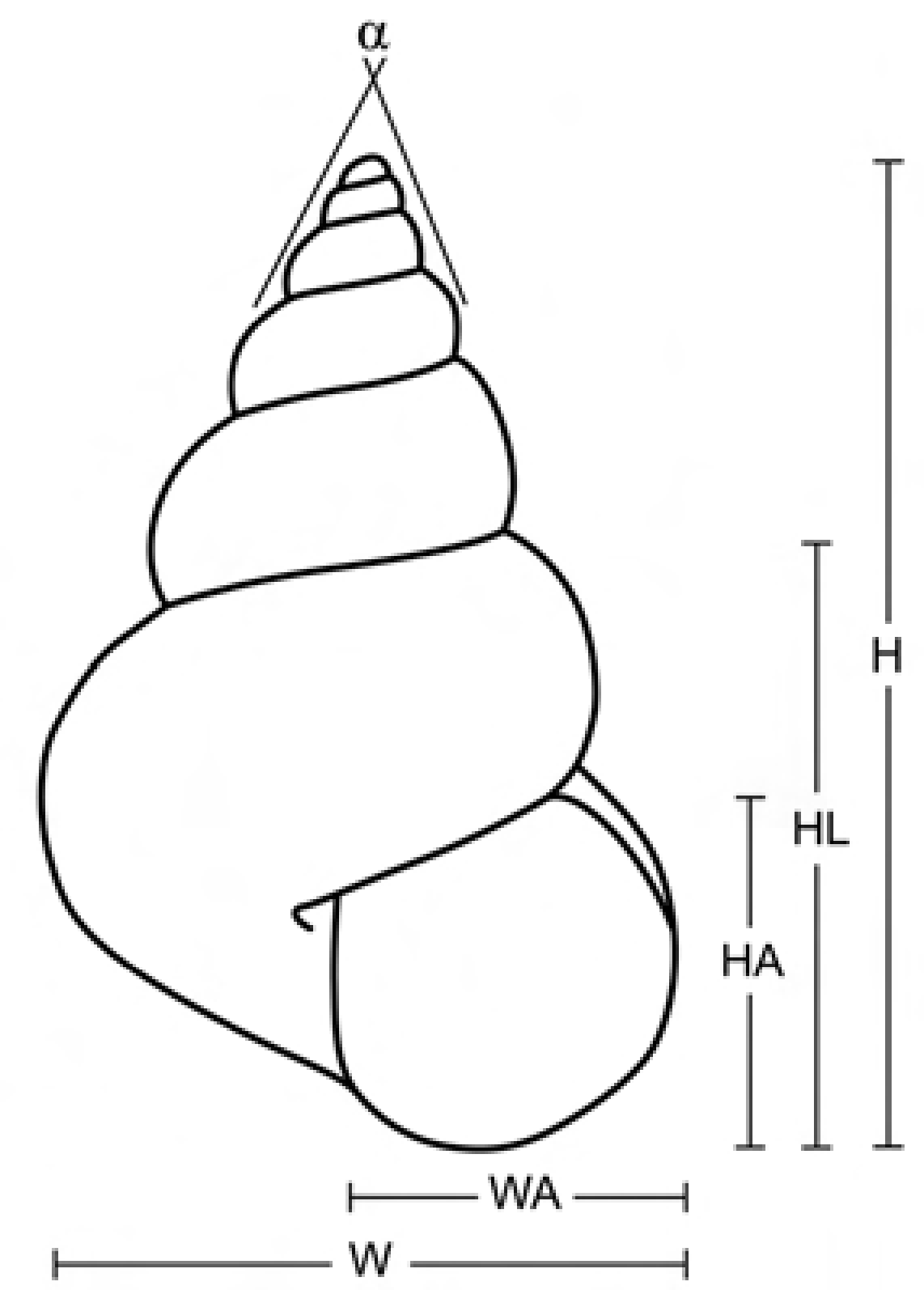
Marls
Calcareous nodule
Bivalves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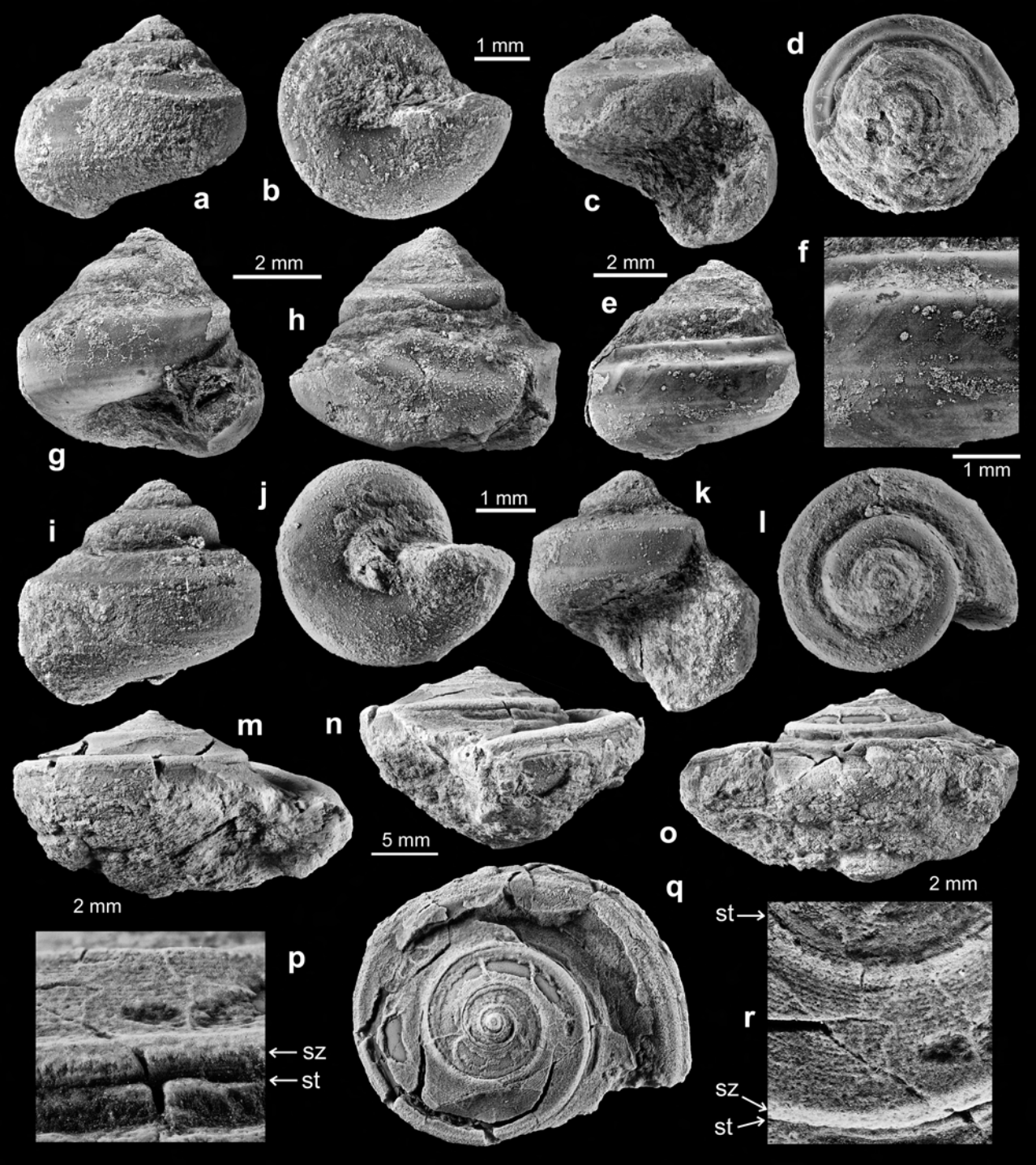
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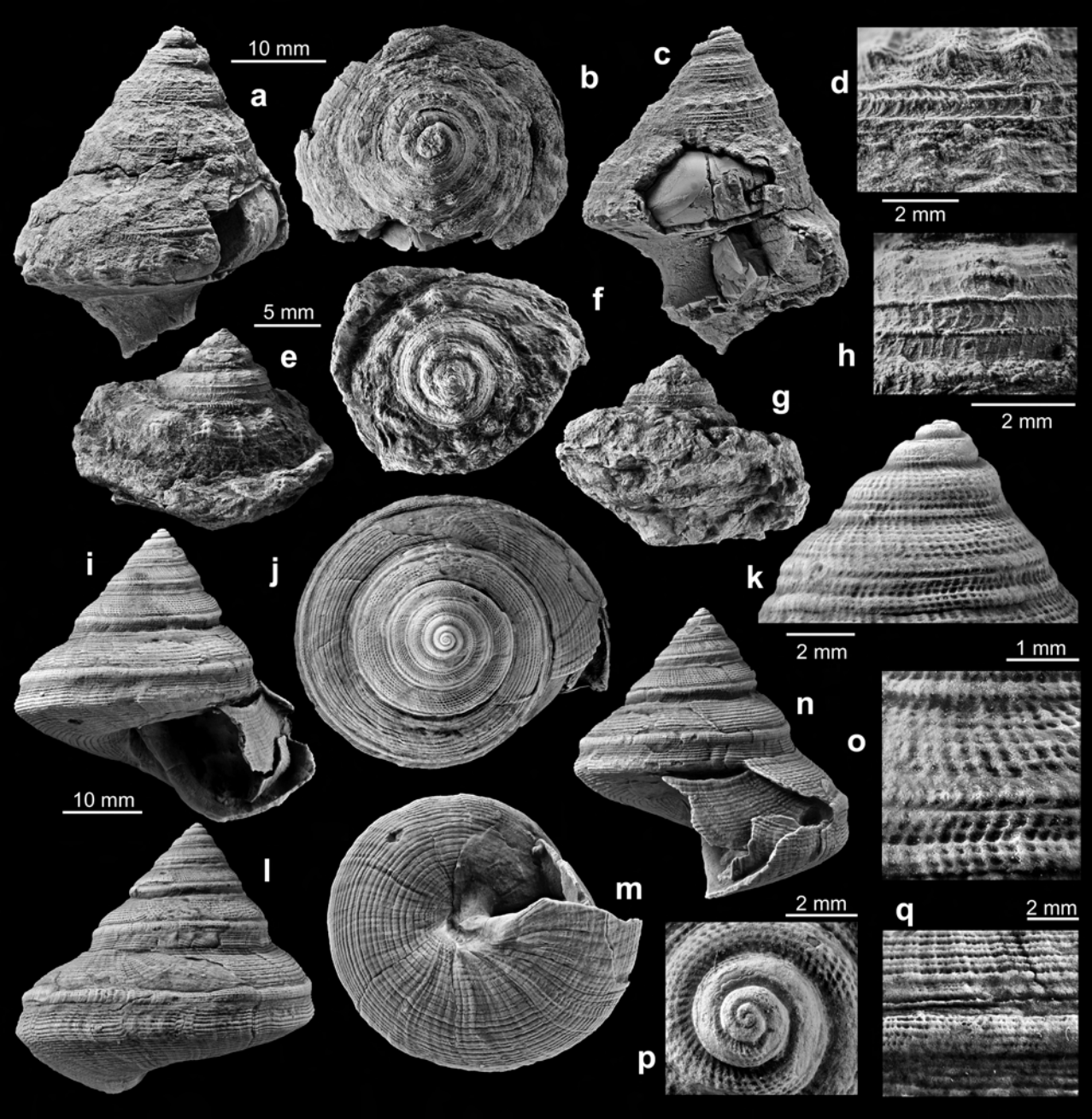
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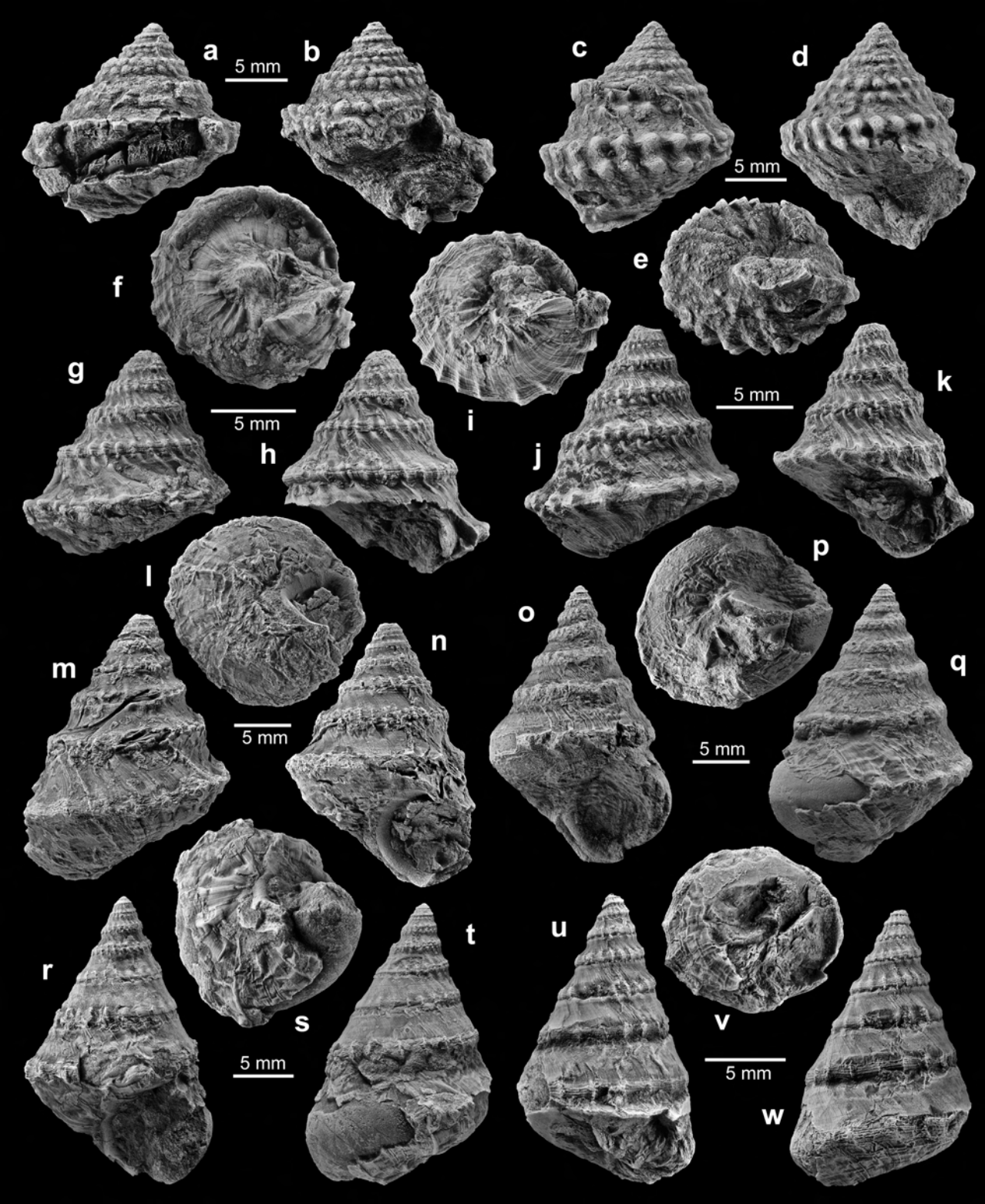
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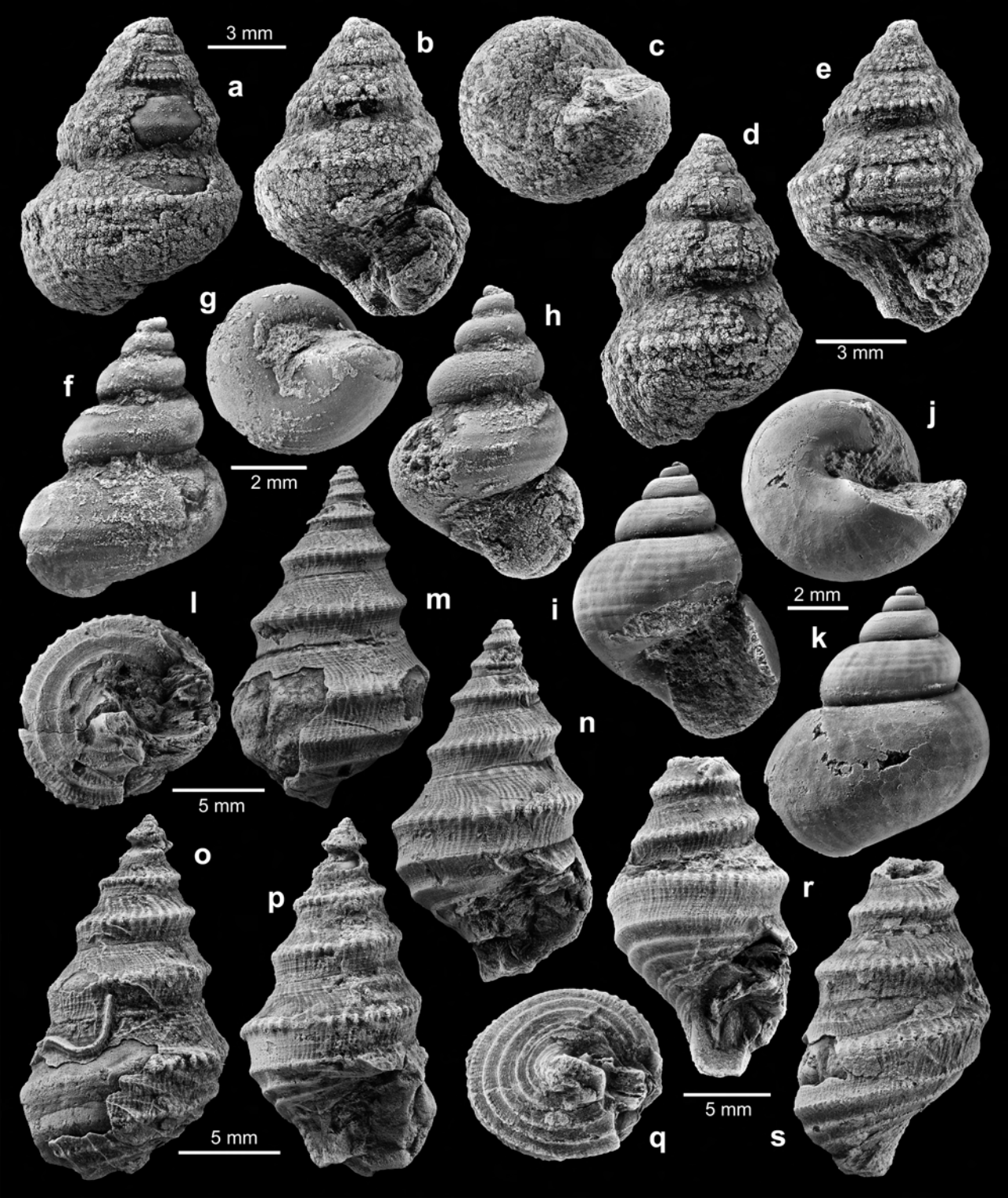
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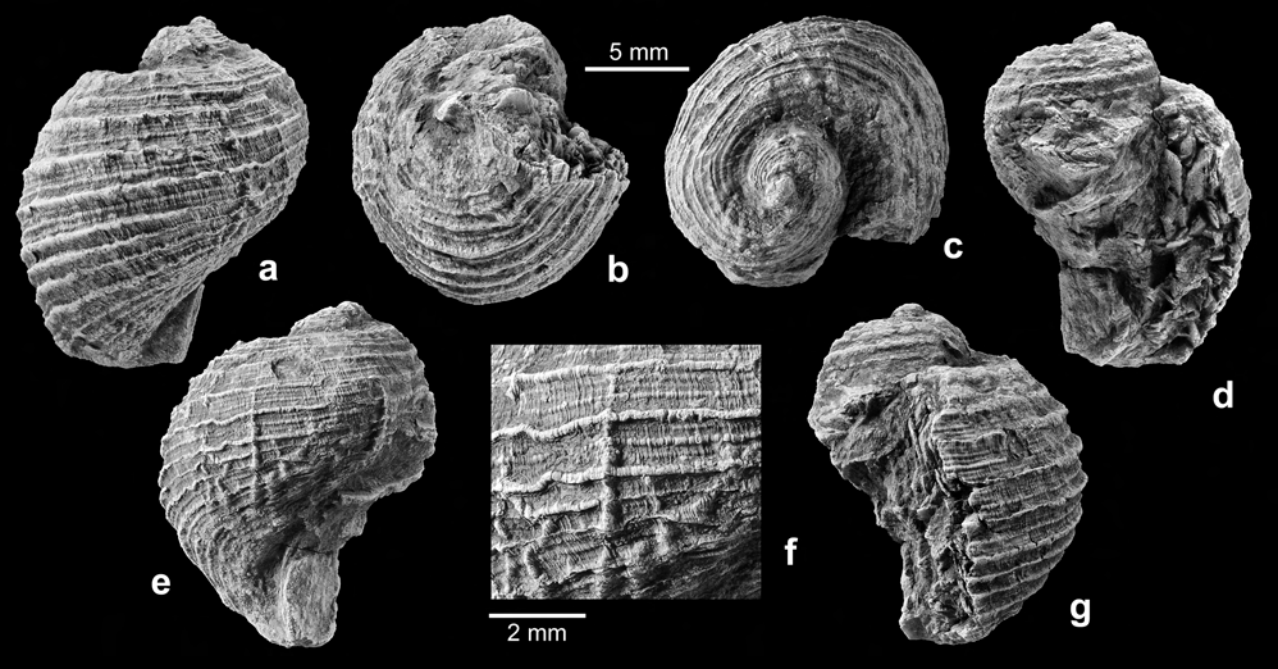
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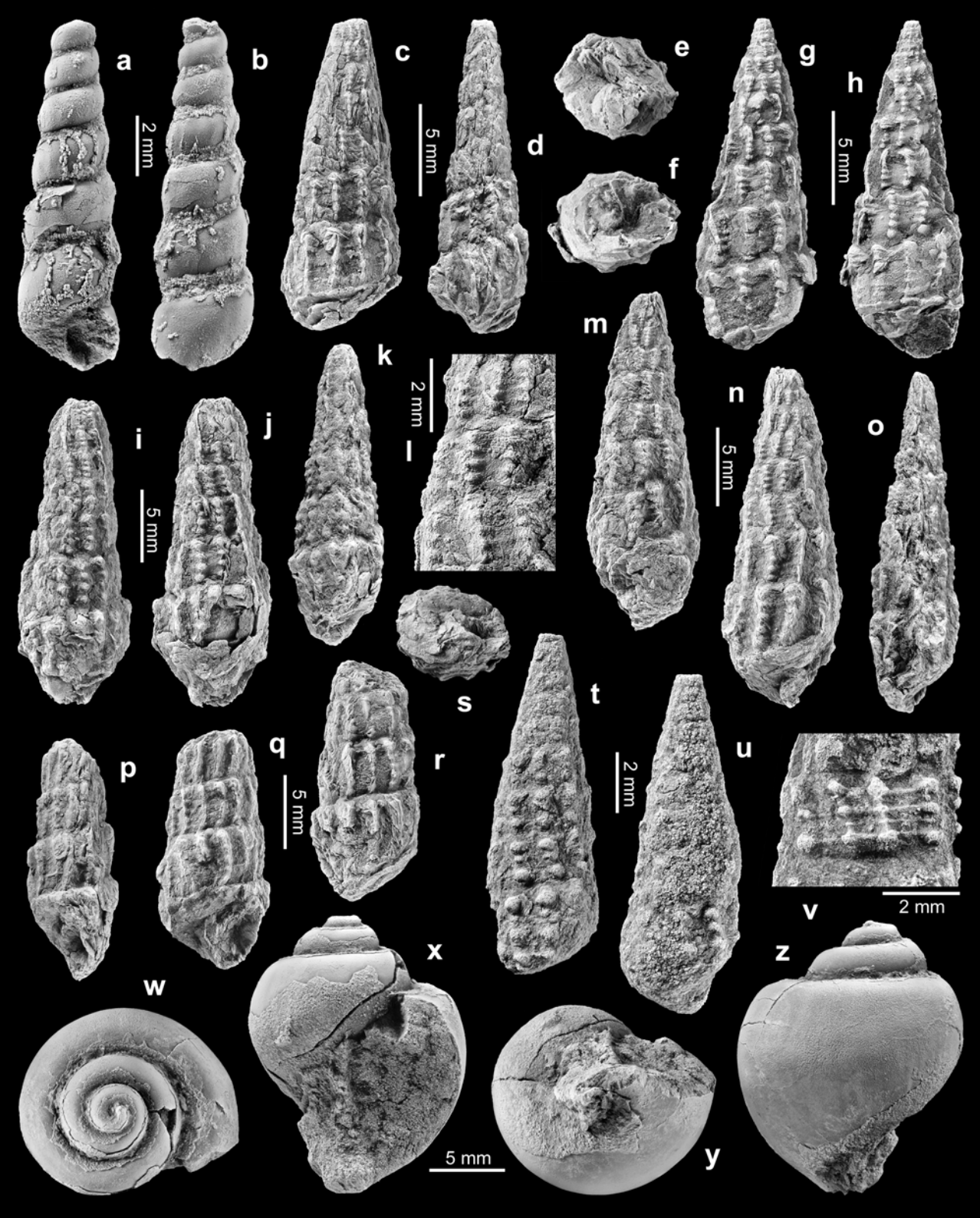
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	CORNUS AND TOURNADOUS SECTIONS																STRATIGRAPHICAL DISTRIBUTION IN OTHER LOCALITIES OF WESTERN EUROPEAN SHELF							
	UPPER PLIENSB.		LOWER TOARCIAN				UPPER TOARCIAN																	
ZONE	Margaritatus	?	Serpentinum		Bifrons		Variabilis			condensed Thouarsense to Dispansum, Insigne subz. p.p.	Dispansum		Pseudoradiosa		Aalensis		Upper Sinemurian	Pliensbachian		Toarcian		Aalenian		Lower Bajocian
SUBZONE	Gibbosus		Elegantulum	Falciferum	Sublevisoni	Bifrons	Variabilis	Illustris	Vitiosa		Insigne	Gruneri	Levesquei	Pseudoradiosa	Mactra	Fluitans		Lower	Upper	Lower	Upper	Lower	Upper	
Procerithium pseudocostellatum															*					?	—	—		
Neritopsis philea															*					?	—	—	—	
Pleurotomaria escheri															*				—	—		—		
Eucycloidea tenuistria					?	*	?			*	*	*	*		*	*				—	—	—		—
Costatrochus subduplicatus					?	*	?			*	*		*		*	*				—	—	—		
Ampullospira pelops						*														?	—			
Cryptaulax armata						*														?	—	—		
Bathrotomaria kronzwilmesorum						*																		
Katosira sp.					*																			
Eucyclus elegans					*														—					
Eucyclus escheri					*													—	—			—		
Sisenna canalis					*														—	—				
Ooliticia? cf. *cyclostoma*	*																		—	(*O.? cyclostoma*)				
Pleurotomaria amalthei	*																		—					
Angulomphalus expansus	*																—	—	—					

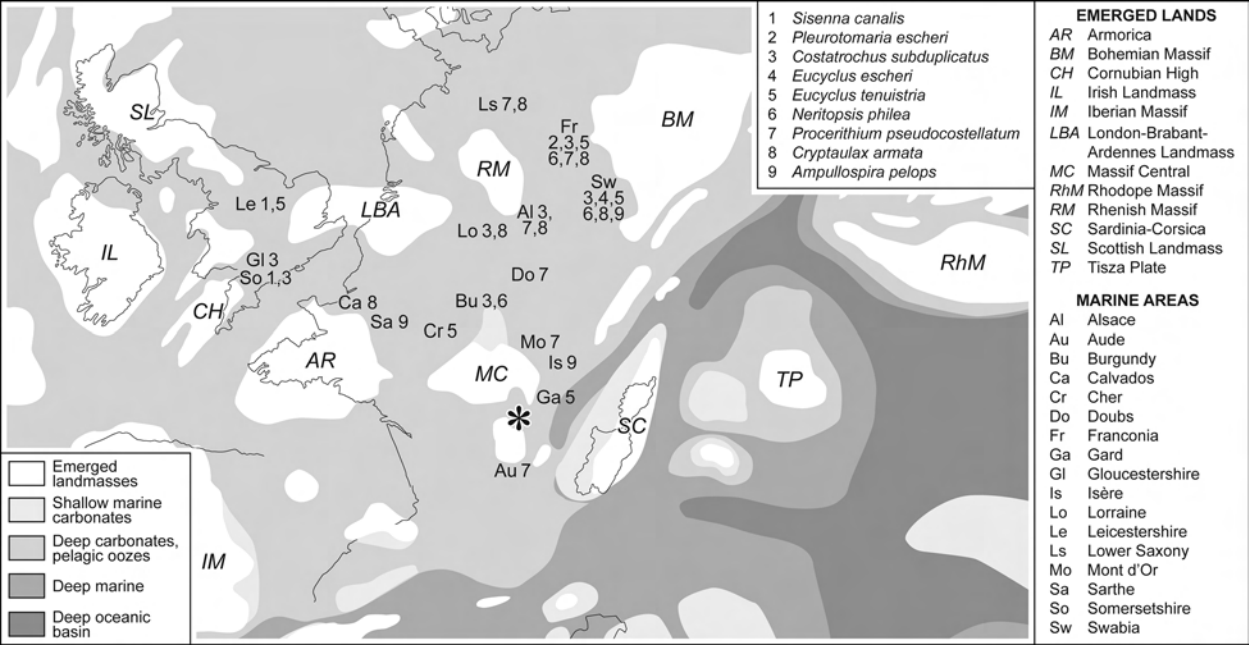
1 Sisenna canalis
2 Pleurotomaria escheri
3 Costatrochus subduplicatus
4 Eucyclus escheri
5 Eucyclus tenuistria
6 Neritopsis philea
7 Procerithium pseudocostellatum
8 Cryptaulax armata
9 Ampullospira pelops
EMERGED LANDS
AR Armorica
BM Bohemian Massif
CH Cornubian High
IL Irish Landmass
IM Iberian Massif
LBA London-Brabant-Ardennes Landmass
MC Massif Central
RhM Rhodope Massif
RM Rhenish Massif
SC Sardinia-Corsica
SL Scottish Landmass
TP Tisza Plate
MARINE AREAS
Al Alsace
Au Aude
Bu Burgundy
Ca Calvados
Cr Cher
Do Doubs
Fr Franconia
Ga Gard
Gl Gloucestershire
Is Isère
Lo Lorraine
Le Leicestershire
Ls Lower Saxony
Mo Mont d'Or
Sa Sarthe
So Somersetshire
Sw Swabia
Emerged landmasses
Shallow marine carbonates
Deep carbonates, pelagic oozes
Deep marine
Deep oceanic basin
SL
IL
CH
AR
IM
LBA
RM
BM
MC
SC
TP
RhM
Ls 7,8
Fr 2,3,5 6,7,8
Sw 3,4,5 6,8,9
Le 1,5
Al 3, 7,8
Lo 3,8
Gl 3
So 1,3
Do 7
Ca 8
Sa 9
Bu 3,6
Cr 5
Mo 7
Is 9
Ga 5
Au 7

Table 1. Measurements of the most representative specimens studied.

Specimen	H	HL	HA	W	WA	α
Sisenna canalis (Münster in Goldfuss, 1844)						
MNHNL QH578	5.2*	3.7	-	5.6	-	-
MNHNL QH579	4.0*	3.4	2.5	3.9	1.9	94°
MNHNL QH580	3.6*	3.0	2.2	3.8	1.7	102°
Angulomphalus expansus (Sowerby, 1821)						
MNHNL QH619	10.4*	-	-	24.2	8.6	132°
Pleurotomaria amalthei Quenstedt, 1858						
UBGD 278805	29.1*	-	-	23.8*	-	67°
Pleurotomaria escheri Goldfuss, 1844						
MNHNL QH581	13.9*	-	-	18.3*	-	110°
Bathrotomaria kronzwilmesorum sp.n.						
MNHNL QH620	36.9	24.7	14.6	38.1	18.2	78°
Costatrochus subduplicatus (d'Orbigny, 1850)						
MNHNL QH582	25.6*	16.5	11.4	-	-	-
MNHNL QH584	24.4	14.7	10.8	-	-	-
MNHNL QH585	25.0	14.6	9.2	-	-	-
MNHNL QH586	24.8	16.3	10.4	17.8	9.5	55°
MNHNL QH587	21.1	13.4	8.9	17.9	8.1	60°
MNHNL QH588	24.8	-	10.8	18.1	10.8	55°
MNHNL QH589	27.5	16.4	12.2	18.7*	10.8*	56°
MNHNL QH590	17.9	11.8	-	14.2	7.5	60°
MNHNL QH596	22.6	15.4	10.1	17.6	-	54°
MNHNL QH597	15.2*	9.6	6.1	13.0	6.1	59°
MNHNL QH617	17.1	12.4	9.1	17.2	8.7	88°
MNHNL QH618	16.7	11.6	8.0	14.1	6.0	74°
Eucyclus escheri (Münster in Goldfuss, 1844)						
MNHNL QH599	12.1*	8.4	5.4	8.5	3.5	50°
MNHNL QH600	10.6*	6.5*	3.5*	7.6*	-	-
Eucyclus elegans (Münster in Goldfuss, 1844)						
MNHNL QH601	7.8*	4.9	2.7	5.2	2.9	50°
Ooliticia? cf. *cyclostoma* (Benz in Zieten. 1832)						
UBGD 278819	10.0*	7.5	4.9	7.6	4.2	66°
Eucycloidea tenuistria (Münster in Goldfuss, 1841)						
MNHNL QH603	-	-	-	10.8	5.4	49°
MNHNL QH608	14.0	9.4	5.4	9.2	4.9	55°
MNHNL QH609	22.1*	14.6	9.8	14.3	8.6	52°
MNHNL QH610	15.7*	-	-	10.0	-	-
UBGD 278820	-	13.2	8.7	-	-	-
UBGD 278822	17.4	11.1	7.2	10.2	5.5	50°
Neritopsis philea d'Orbigny, 1850						
UBGD 278835	17.7*	16.8	12.2	13.3	7.6	-
Katosira sp.						
MNHNL QH611	11.6*	4.3*	2.2*	3.4*	1.8*	-
Procerithium pseudocostellatum (d'Orbigny, 1850)						
UBGD 278836	17.1*	-	-	6.4*	-	-
UBGD 278838	19.9*	-	-	7.0*	-	23°
Cryptaulax armata (Goldfuss, 1843)						
MNHNL QH614	11.5*	4.3	2.5	3.9	-	-
Ampullospira pelops (d'Orbigny, 1850)						
UBGD 278841	17.2*	15.1	12.5	13.5	8.2	99°

Linear measurements are in millimetres. The asterisk (*) indicates measurements made on incomplete specimens. See Fig. 3 for the abbreviations of the dimensions.